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FLORISTIC AND ZONATION STUDIES OF SEAWEEDS FROM MOUNT DESERT ISLAND, MAINE: AN HISTORICAL COMPARISON

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ABSTRACT. Based upon recent collections at 28 sites plus historical data from the last century, the macroalgal flora of Mount Desert Island consists of 41 Chlorophyceae, 50 Phaeophyceae, and 55 Rhodophyceae. Previously, 121 seaweeds were recorded from Mount Desert Island and 113 taxa were found during present sampling. A comparison of the two time periods shows 88 taxa in common or a 75% similarity. Varying percent similarity patterns are evident when historical and present collections at Otter Cliffs (68%), Seal Harbor (43%), and the Seawall-Southwest Harbor areas (54%) are compared. The reduced values for Seal Harbor may reflect anthropogenic effects, while the other values may represent varying levels of taxonomic characterization and/or temporal variability of floras. Pronounced habitat diversity on Mount Desert Island probably causes the relatively low intra-island similarity patterns ($\bar{x}$ = 36.8 ± 7.6%), while interisland comparisons of other Northwest Atlantic islands are much higher (ca. 51.0–92.0%, $\bar{x}$ = 72.3% ± 6.0%). In comparing species richness around Mount Desert Island, the largest numbers of taxa occur on the exposed coasts at Otter Cliffs and Seawall that experience intense wave activity, while the lowest numbers occur at several sheltered sites.

Zonation patterns at three representative sites (exposed Otter Cliffs, protected Otter Cove, and sheltered Thompson Island) show pronounced localized differences. The biological zones at Otter Cliffs exceed mean tidal amplitude, and patterns of species richness there are also higher than at the other two Mount Desert sites. Green algae show the most conspicuous decrease in species richness with increasing shelter. Of the 32 intertidal species in common with a 1928 zonation study at Otter Cliffs, 13 showed a conspicuous reduction in their upper distributional limits (0.5 to 2.0 m), while none showed an upward expansion. Such reductional patterns may reflect either a general warming trend in the Gulf of Maine or the effects of air pollution during intertidal exposure.

Key Words: seaweeds, history, ecology, Mount Desert Island, Maine, Gulf of Maine

Mount Desert Island, which is the largest insular habitat (Figure 1, 2) on Maine's extensive and indented coastline (Platt 1996; Simpson 1987), has a long and unique phycological history. Rand and Redfield (1894) produced an initial catalogue of its plants (phanerogamic and cryptogamic), as well as a synopsis of the island's ecology, geology, and postglacial history based upon studies initiated during the early 1880s. Two noted phycologists, Frank Shipley Collins and Isaac Holden, studied the algae, recording approximately 100 taxa from the exposed, eastern shoreline and nearby Cranberry Isles (Collins 1894). Several other new taxa were recorded in *Phycotheca Boreali-Americana*, the largest exsiccata of seaweeds ever published (cf. Setchell 1925; Taylor 1957). Taylor (1921) listed a few additional seaweeds based upon summer collections during 1915 and 1920. Johnson and Skutch (1928a, b, c) described the species composition, zonation, and ecology of intertidal algae at Otter Cliffs, an exposed promontory on the eastern side of the island (site 11; Figure 2, 3A). It is still one of the most significant studies of its kind for any part of the Maine coastline (Mathieson et al. 1991).

In the present study, the floristic composition and zonation of seaweeds from Mount Desert Island, Maine, are described utilizing recent and historical collections from the last century plus detailed zonation comparisons at Otter Cliffs (Johnson and Skutch 1928a, b, c). The seaweed zonation is also compared with recent studies at Bald Head Cliff, York, Maine (Femino and Mathieson 1980), and Jaffrey Point, Newcastle, New Hampshire (Mathieson et al. 1981). As noted by Barry et al. (1995), the diverse impacts of man on coastal resources are often difficult (impossible) to assess because few detailed "baselines" exist for comparisons. With Mount Desert's long phycological history and the fact that it now contains one of the most popular national parks in the United States (Acadia), such comparisons can be used to assess shifts in the macroalgal communities in the future. The specific objectives of our field studies are fourfold: (1) to assess the number and types of seaweeds at diverse sites around the island; (2) to compare present and previously documented patterns of species richness and composition at three sites; (3) to compare present patterns of zonation among three Mount Desert sites, as well as two others in southern Maine and New Hampshire with variable wave exposure; and (4) to compare present and previous patterns of seaweed zonation at Otter Cliffs, Bar Harbor.

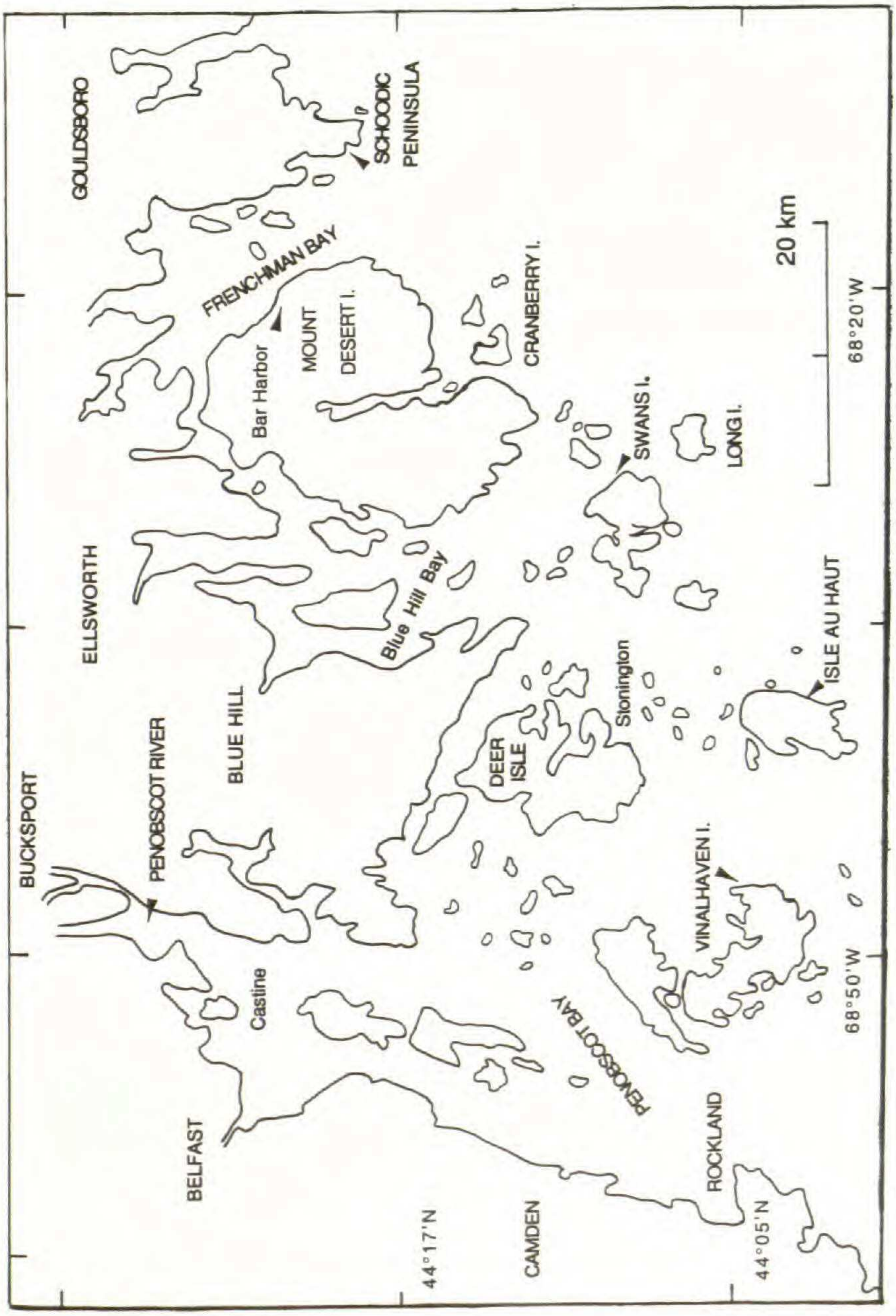

Figure 1. Mid-coastal Maine between Rockland (Penobscot Bay) and the Schoodic Peninsula, including Mount Desert Island.

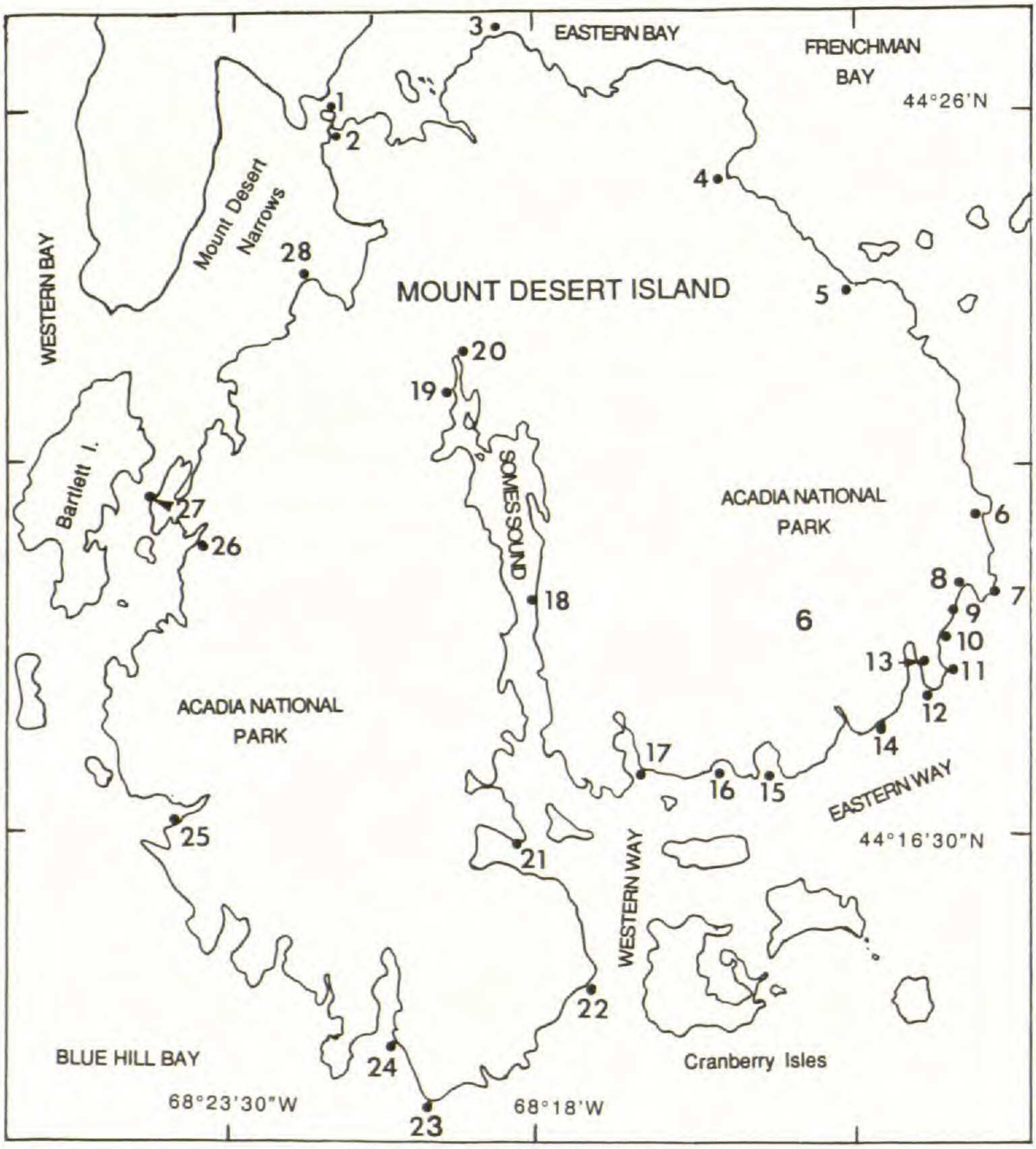

Figure 2. Mount Desert Island showing the location of 28 recent collecting sites.

MATERIALS AND METHODS

Floristic studies. In assessing present floristic patterns on Mount Desert Island, extensive year-round collections and observations of intertidal and shallow subtidal seaweeds were made at 28 locations (Figure 2; Table 1; Appendix). The sites were established clockwise around the island, starting at Thompson Island on Mount Desert Narrows (site #1) and ending at Indian Point on Western Bay (site #28). Old House Cove (#2) and Indian Point (#28) are closest to Thompson Island. Four primary considerations were important in establishing these study sites: (1) acces-

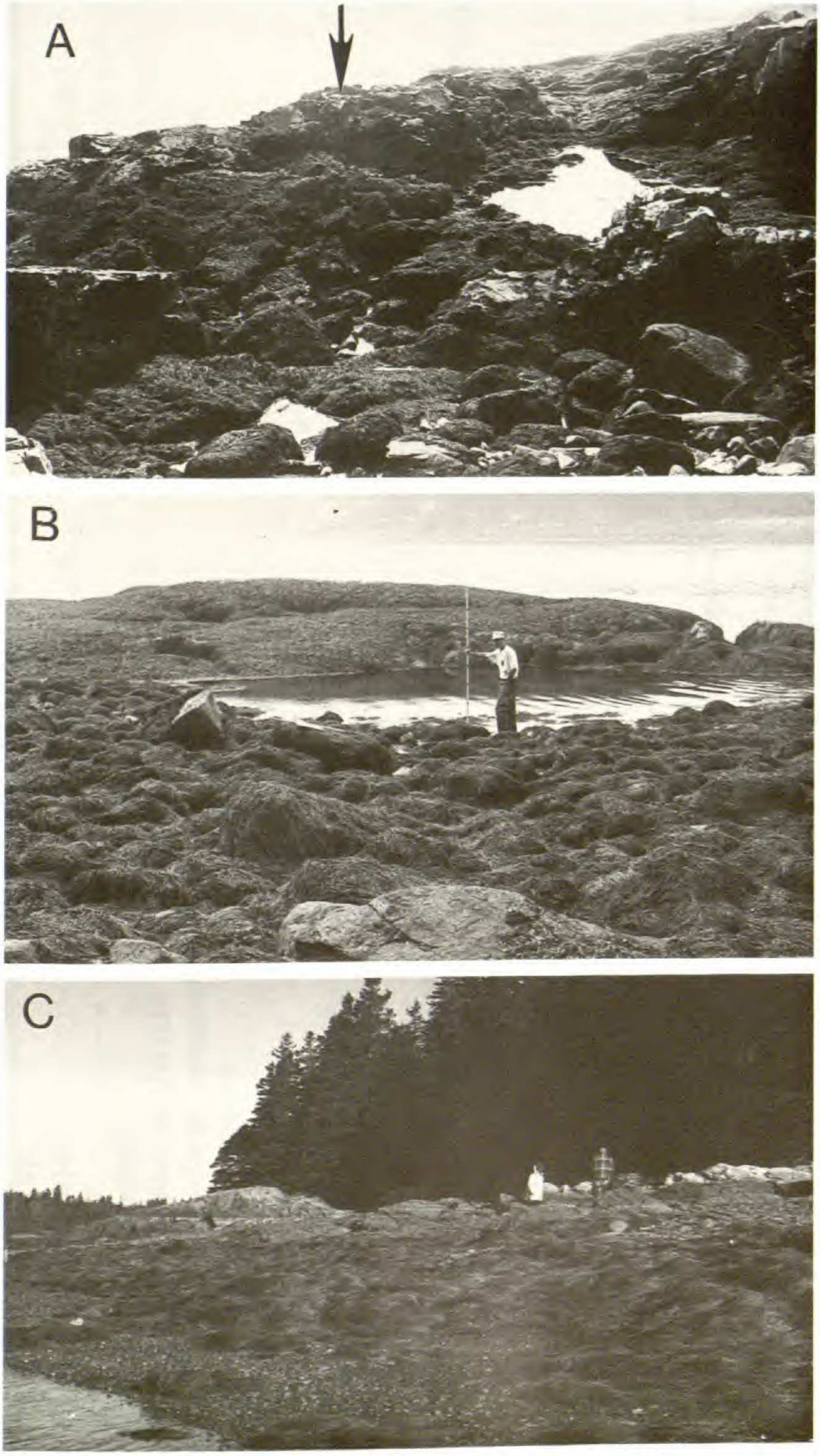

Figure 3. Three Mount Desert habitats where zonation studies were conducted during 1996. (A) Otter Cliffs: an exposed site showing Johnson and Skutch's (1928a) bench mark (arrow) plus a large tide pool. (B) Otter Cove: a sheltered site with a dense growth of fucoid algae. CJD is holding a stadia rod near the extreme lower intertidal region. (C) Thompson Island: a protected habitat with scattered boulders, abundant *Ascophyllum nodosum*, a fringing *Spartina* salt marsh (ACM standing), and contiguous terrestrial vegetation.

Table 1. Historical and recent collections from Mount Desert Island and adjacent Cranberry Isles, plus percent occurrence at twenty-eight present-day sites. See Appendix for numerical site designation, plus dates of collections and collectors; X = recorded by Collins (1894) as being common but no specific locations given.

	Historical Collections	Present Collections (% Occurrence)
BACILLARIOPHYCEAE		
Berkeleya rutilans (Trentopohl) Grünow		3, 6–8, 10–13, 15–17, 22, 23, 26 (50%)
TOTAL DIATOM TAXA	0	1
COMBINED TOTAL DIATOM TAXA (1)		
CHLOROPHYCEAE		
Blidingia minima (Nägeli ex Kützing) Kylin	11, 15, 21	6, 7, 11, 13, 14, 16, 17 (25%)
Bolbocoleon piliferum N. Pringsheim	15	(0%)
Capsosiphon fulvescens (C. Agardh) Setchell et N. L. Gardner	15, 16	6, 12, 19, 20 (11%)
Capsosiphon groenlandicum (J. Agardh) K. L. Vinogradova	14a	10 (4%)
Chaetomorpha aerea (Dillwyn) Kützing	17a	14 (4%)
Chaetomorpha brachygona Harvey		14 (4%)
Chaetomorpha linum (O. F. Müller) Kützing		2, 15, 22, 26 (11%)
Chaetomorpha melagonium (Weber et D. Mohr) Kützing	11, 17a, 21, 22	6, 7, 10, 11, 14, 22 (21%)
Chaetomorpha picquotiana Montagne ex Kützing		2, 15, 17 (11%)
Chlorochytrium schmitzii Rosenvinge	15	(0%)
Cladophora rupestris (L.) Kützing	22	(0%)
Cladophora sericea (Hudson) Kützing	11, 15, 17a, 21, 22	7, 9, 11–14, 21, 24, 26 (32%)
Cladophora vagabunda (L.) C. Hoek	16, 17a, 21	(0%)
"*Codiolum petrocelidis* Kuckuck"	14a, 15	14, 22, 23 (11%)
"*Codiolum pusillum* (Lyngbye) Kjellman"	11, 15, 22	11–13, 22 (14%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Enteromorpha clathrata (Roth) Greville	15, 16	6, 7, 12, 14, 22 (18%)
Enteromorpha compressa (L.) Nees	11, 15, 21	13 (4%)
Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh ssp. *paradoxa* (Dillwyn) Bliding	15, 17a	(0%)
Enteromorpha intestinalis (L.) Nees	15, 21	5–16, 19, 22, 23 (54%)
Enteromorpha linza (L.) J. Agardh	15	5, 10, 11 (11%)
Enteromorpha prolifera (O. F. Müller) J. Agardh	17a	11, 12, 24 (11%)
Enteromorpha torta (Mertens in Juerg.) Reinbold		20, 26 (7%)
Epicladia flustrae Reinke		13, 23 (7%)
"*Gomontia polyrhiza* (Lagerheim) Bornet et Flahault"	15	(0%)
Microspora pachyderma (Wille) Lagerheim		7, 12, 16, 17, 20–22, 26, 28 (32%)
Monostroma grevillei (Thuret) Wittrock	11, 17a	3–8, 10, 12, 14–18, 22, 23, 25, 26, 28 (61%)
Percursaria percursa (C. Agardh) Bory	15, 21, X	2, 21, 26 (11%)
Pilinia endophytica Collins		3, 15 (7%)
Prasiola stipitata Suhr in Jessen		11 (4%)
Protomonostroma undulatum (Wittrock) K. L. Vinogradova f. *pulchrum* (Farlow) M. Wynne	22	5, 8, 10, 12, 14, 16, 22 (25%)
Rhizoclonium riparium (Roth) Kützing ex Harvey	15, 21	2, 4, 16, 17, 20, 24, 26, 28 (29%)
Rhizoclonium tortuosum (Dillwyn) Kützing	11, 21a	5, 6, 10–14, 22 (29%)
Spongomorpha aeruginosa (L.) C. Hoek	14a, 15, 17a	(0%)
Spongomorpha arcta (Dillwyn) Kützing	11, 15, 21, 21a, 22	5–15, 22 (43%)
Spongomorpha spinescens Kützing	11, 15, 21, 22	11, 21 (8%)
Ulothrix flacca (Dillwyn) Thuret in Le Jolis	11, 13a	(0%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Ulothrix speciosa (Carmichael ex Harvey in Hooker) Kützing		5, 7, 10, 16, 17, 21 (21%)
Ulva lactuca L.	11, 15	4–8, 10–17, 22 (46%)
Ulvaria obscura (Kützing) Gayral	15	6, 10–15, 19, 22, 23 (36%)
Urospora penicilliformis (Roth) Areschoug	11, 17a	5–18, 20, 22, 23, 26 (64%)
Urospora wormskjoldii (Mertens in Hornemann) Rosenvinge	11	7, 8, 22 (11%)
TOTAL GREEN ALGAL TAXA	32	33
COMBINED TOTAL GREEN ALGAL TAXA (41)		
PHAEOPHYCEAE		
Agarum clathratum Dumort.	11, 15, 21, 22, X	7, 13–15, 22, 23 (21%)
Alaria esculenta (L.) Greville	11, 15, 21, 22	6–8, 10–12, 14, 22, 23 (32%)
Ascophyllum nodosum (L.) Le Jolis	11, 15, X	1, 2, 4–8, 10–28 (93%)
Ascophyllum nodosum (L.) Le Jolis ecad *scorpioides* (Reinke) Hauck		1, 2, 16, 19, 20, 24, 26, 28 (29%)
Asperococcus fistulosus (Hudson) Hooker	15	(0%)
Chorda filum (L.) Stackhouse	15, 17a	(0%)
Chorda tomentosa Lyngbye		14 (4%)
Chordaria flagelliformis (O. F. Müller) C. Agardh	11, 15, 21, 22	11, 12, 14 (11%)
Desmarestia aculeata (L.) J. V. Lamouroux	17a, 21, 22	15 (4%)
Desmarestia viridis (O. F. Müller) J. V. Lamouroux	15, 17a	8, 15, 16 (11%)
Dictyosiphon foeniculaceus (Hudson) Greville	15, 17, 17a, 21, 22	6, 7, 11, 12 (14%)
Dictyosiphon macounii Farlow	17a	(0%)
Ectocarpus fasciculatus Harvey	13a, 15, 17a, 21, 22	7, 11, 17, 22 (14%)
Ectocarpus siliculosus (Dillwyn) Lyngbye	15, 17a, 21	14 (4%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Elachista chondrii Areschoug		11 (4%)
Elachista fucicola (Velley) Areschoug	11, 14a, 15, 21, 22, X	5, 6, 10–13, 15, 17, 22, 28 (36%)
Eudesme virescens (Carm. ex Harvey in Hooker) J. Agardh	15, 17a	(0%)
Fucus distichus (L.) emend. Powell ssp. *anceps* (Harvey et Ward ex Carruthers) Powell		10, 14 (7%)
Fucus distichus (L.) emend. Powell ssp. *distichus* Powell	5a, 11, 15	5–7, 9–12, 14, 15, 22, 23 (39%)
Fucus distichus (L.) emend. Powell ssp. *edentatus* (Bach. Pyl.) Powell	11, 17a, 22	6–12, 15, 22, 23 (36%)
Fucus distichus (L.) emend. Powell ssp. *evanescens* (C. Agardh) Powell	11, X	11, 13, 15, 17 (14%)
Fucus spiralis L.	21	1, 5, 6, 10–15, 17, 18, 22–24 (50%)
Fucus vesiculosus L.	11, 21, X	1, 2, 4–13, 15–20, 22–28 (86%)
Fucus vesiculosus L. f. *limicola* Collins		1, 2, 28 (11%)
Gononema aecidioides (Rosenvinge) P. M. Pedersen	21	(0%)
Laminaria digitata (Hudson) J. V. Lamouroux	11, 15, 17a, 22, X	6, 7, 10–12, 14, 16, 22 (29%)
Laminaria longicruris Bach. Pyl.	21	17 (4%)
Laminaria saccharina (L.) J. V. Lamouroux	17a, X	10–13, 22, 23 (21%)
Leathesia difformis (L.) Areschoug	11, 15, 22	11 (4%)
Melanosiphon intestinalis (Saunders) Wynne		28 (4%)
Myrionema corunnae Sauvageau		14, 22 (7%)
Myrionema magnusii (Sauvageau) Loiseaux	15, 17a	(0%)
Myrionema strangulans Greville	14a, 15, 17a	(0%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Petalonia fascia (O. F. Müller) Kuntze	11, 15, 16	3–7, 10, 12–18, 21–23, 26 (61%)
Petroderma maculiforme (Wollny) Kuckuck		3, 16, 25 (11%)
Pilayella littoralis (L.) Kjellman	11, 15, X	3–5, 8, 11–18, 20, 26, 28 (54%)
Pseudolithoderma extensum (P. et H. Crouan) S. Lund		13, 20 (7%)
Punctaria latifolia Greville	15, 17a, 21	(0%)
Punctaria tenuissima (C. Agardh) Greville	15, 17a, 21	(0%)
"*Ralfsia bornetii* Kuckuck"	15	3, 4, 7, 15, 16, 18, 23 (25%)
"*Ralfsia clavata* (Carmichael) Crouan *sensu* Farlow"	15	2, 11, 15, 21, 28 (18%)
Ralfsia fungiformis (Gunnerus) Setchell et N. L. Gardner	21, 22	(0%)
Ralfsia pusilla (Strömfelt) Batters	21, 22	(0%)
Ralfsia verrucosa (Areschoug) J. Agardh	11, X	1, 4, 5, 10, 11, 15, 16, 20–23, 25, 27, 28 (50%)
Saccorhiza dermatodea (Bach. Pyl.) J. Agardh	11, 14a, 15, 22	10, 11, 14 (11%)
Scytosiphon simplicissimus (Clemente) Cremades	11, 15, 21, X	3–7, 10–18, 21–23, 26–28 (71%)
Sphacelaria cirrosa (Roth) C. Agardh	17a	6, 11 (7%)
Sphacelaria radicans (Dillwyn) C. Agardh	15	(0%)
Spongonema tomentosum (Hudson) Kützing		11 (4%)
Stictyosiphon griffithsianus (Le Jolis) Holmes et Batters	17a	(0%)
TOTAL BROWN ALGAL TAXA	40	37
COMBINED TOTAL BROWN ALGAL TAXA (50)		
RHODOPHYCEAE		
Ahnfeltia plicata (Hudson) Fries	15, 22	7, 11, 12, 22 (14%)
Antithamnionella floccosa (O. F. Müller) Whittick	11	14, 17 (7%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Audouinella alariae (H. Jónsson) Woelkerling	15, 22	(0%)
Audouinella daviesii (Dillwyn) Woelkerling	16, 17a	(0%)
Audouinella membranacea (Magnus) Papenfuss	15	13, 23 (7%)
Audouinella purpurea (Lightfoot) Woelkerling	15, 17a, 21a	6, 11, 14 (11%)
Audouinella secundata (Lyngbye) P. Dixon in M. Parke et P. Dixon		5, 11, 12, 22 (14%)
Bangia atropurpurea (Roth) C. Agardh	11, 15	6–8, 10, 12, 14, 15, 17, 22 (32%)
Callithamnion tetragonum (Withering) S. F. Gray		2 (4%)
Callophyllis cristata (C. Agardh) Kützing	15	10, 15, 22 (11%)
Ceramium deslongchampii Chauvin ex Duby	15, 22	6, 10 (7%)
Ceramium nodulosum (Lightfoot) Ducluzeau	11, 15, 21, 22	6–8, 10–12, 14, 15, 22 (32%)
Chondrus crispus Stackhouse	5a, 11, 15, X	2, 4–18, 22–24, 26–28 (79%)
Choreocolax polysiphoniae Reinsch	15	12 (4%)
Clathromorphum circumscriptum (Strömfelt) Foslie	11, 15, 22, X	4, 5, 7, 11, 13, 15, 16, 22, 23 (32%)
"*Conchocelis rosea* Batters"	15	(0%)
Corallina officinalis L.	5a, 11, 15, 17, 21, 21b, 22	5–7, 9–14, 16, 22, 23 (43%)
Cystoclonium purpureum (Hudson) Batters	15, 17a	15, 23 (7%)
Devaleraea ramentacea (L.) Guiry	11, 15, 22	6–8, 10–12, 14, 15, 22, 23 (36%)
Dumontia contorta (S. G. Gmelin) Ruprecht	22	1, 4, 7–9, 13, 15–18, 22, 23, 28 (46%)
Erythrotrichia carnea (Dillwyn) J. Agardh		13 (4%)
Fimbrifolium dichotomum (Lepechin) G. I. Hansen	15, 17a, 22	(0%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Gloiosiphonia capillaris (Hudson) Carmichael ex Berkeley	15, 16, 22	(0%)
Gymnogongrus crenulatus (Turner) J. Agardh	21, 22	(0%)
Hildenbrandia rubra (Sommerfelt) Meneghini	21, X	1, 2, 7, 11, 13, 15, 17, 20, 22, 25, 27, 28 (43%)
Lithothamnion glaciale Kjellman	17a, 22, X	22, 23 (7%)
Mastocarpus stellatus (Stackhouse in Withering) Guiry in Guiry et al.	11, 15, 17a, 22, X	5–15, 17, 21–23 (54%)
Membranoptera alata (Hudson) Stackhouse	15	22 (4%)
Nemalion helminthoides (Velley in Withering) Batters	15, 22	(0%)
Palmaria palmata (L.) Kuntze	11, 15, 17a, 22, X	6, 7, 10–12, 14, 22, 23 (29%)
"*Petrocelis cruenta* J. Agardh"	11, 14a, 15, 21a, 22, X	6, 8, 11, 13, 14, 22, 23 (25%)
Peyssonnelia rosenvingii F. Schmitz in Rosenvinge	15	(0%)
Phycodrys rubens (L.) Batters	15, 22	22 (4%)
Phyllophora pseudoceranoides (Gmelin) Newroth et A. Taylor		22 (4%)
Phymatolithon lenormandii (Areschoug in J. Agardh) Adey	15, 21, X	2, 7, 15 (11%)
Phymatolithon tenue (Rosenvinge) Düwel et Wegeberg	15	22, 23 (7%)
Plumaria plumosa (Hudson) Kuntze	15, 21	6, 12, 14 (11%)
Pneophyllum fragile Kützing	17a	(0%)
Polyides rotundus (Hudson) Greville	15, 22	(0%)
Polysiphonia flexicaulis (Harvey) Collins	11, 19, 21	1, 13 (7%)
Polysiphonia fucoides (Hudson) Greville	16	8, 15 (7%)
Polysiphonia harveyi J. Bailey	21	2, 11 (7%)
Polysiphonia lanosa (L.) Tandy	11, 15, 21, X	5–8, 10–15, 17, 18, 22, 23 (50%)
Polysiphonia stricta (Dillwyn) Greville	15, 17a	6, 8–12, 14–16, 22, 23 (39%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Porphyra amplissima (Kjellman) Setchell et Hus	15	4 (4%)
Porphyra leucosticta Thuret in Le Jolis	11	6, 8, 10, 12, 22 (18%)
Porphyra linearis Greville		9, 10, 22 (11%)
Porphyra miniata (C. Agardh) C. Agardh	15	(0%)
Porphyra purpurea (Roth) C. Agardh		12 (4%)
Porphyra umbilicalis (L.) J. Agardh	11, 15, 22	5, 6, 8, 10–12, 14, 15, 22 (32%)
Ptilota serrata Kützing	15, 21, 22	16 (4%)
Rhodomela confervoides (Hudson) P. C. Silva	21, 22	5, 10–12, 14, 15, 22 (25%)
Scagelia pylaisaei (Montagne) M. J. Wynne	15	(0%)
Titanoderma corallinae (P. et H. Crouan) Woelkerling, Chamberlain et Silva	29	12 (4%)
Titanoderma pustulatum (J. V. Lamouroux) Woelkerling, Y. M. Chamberlain et P. C. Silva	15	11, 13 (7%)
TOTAL RED ALGAL TAXA	49	43
COMBINED TOTAL RED ALGAL TAXA (55)		
TOTAL SEAWEED TAXA	121	113
COMBINED SEAWEED TAXA (146)		

sibility of shorelines by foot; (2) habitat representation and diversity; (3) coverage of the entire island; and (4) previous historical collections. With the exception of a few localized summer collections made during the mid-1960s, the recent collections were made between 1993 and 1996 (Appendix). We made comprehensive seasonal collections of all conspicuous seaweeds at most sites in order to enumerate spatial and temporal patterns (Druehl 1981). Seaweeds were either pressed immediately or transferred within 24–36 hours to the University of New Hampshire where they were processed and identified. Several references were utilized for identification (Adey and Adey 1973; Bird and McLachlan 1992; Blair 1983; Bliding 1963, 1968; Burrows 1991; Dixon and Irvine 1977; Düwel and Wegeberg 1996; Farlow 1881; Fletcher 1987; Hoek 1963, 1982; Irvine 1983; Irvine and Chamberlain 1994; Kingsbury 1969; Maggs and Hommersand 1993; Schneider and Searles 1991; Sears 1998; Taylor 1957; Villalard-Bohnsack 1995; Webber and Wilce 1971; Woelkerling 1973; Wynne and Heine 1992). The nomenclature primarily follows South and Tittley (1986), except for several recent papers noted above. Collections were documented by depositing approximately 1200 voucher specimens in the Albion R. Hodgdon Herbarium at the University of New Hampshire (NHA).

Collections from the last century were also evaluated (>300 specimens), including those of Frank Shipley Collins and Isaac Holden (cf. Appendix). Many of these are deposited in the Farlow Herbarium (FH) of Harvard University, the Daniel C. Eaton Herbarium of the Peabody Museum at Yale University (YU), and the New York Botanical Garden (NY) and Brooklyn Botanic Garden (BKL). Specimens contained within *Phycotheca Boreali-Americana* are also particularly important in making historical comparisons of Mount Desert's marine algal flora (Setchell 1925; Taylor 1957).

Two floristic assessments of Mount Desert seaweeds are made. First, the number and percentage of taxa in common to each of the 28 present study sites (Figures 4–7) are given, with the latter values (C) determined by using Czekanowski's coefficient (Bray and Curtis 1957; Mathieson et al. 1996). Second, a comparison of historical and present records of taxa at three sites (Otter Cliffs, Seal Harbor, and the Seawall-Southwest Harbor area) is given, as well as for Mount Desert Island as a whole (Figure 2, 8).

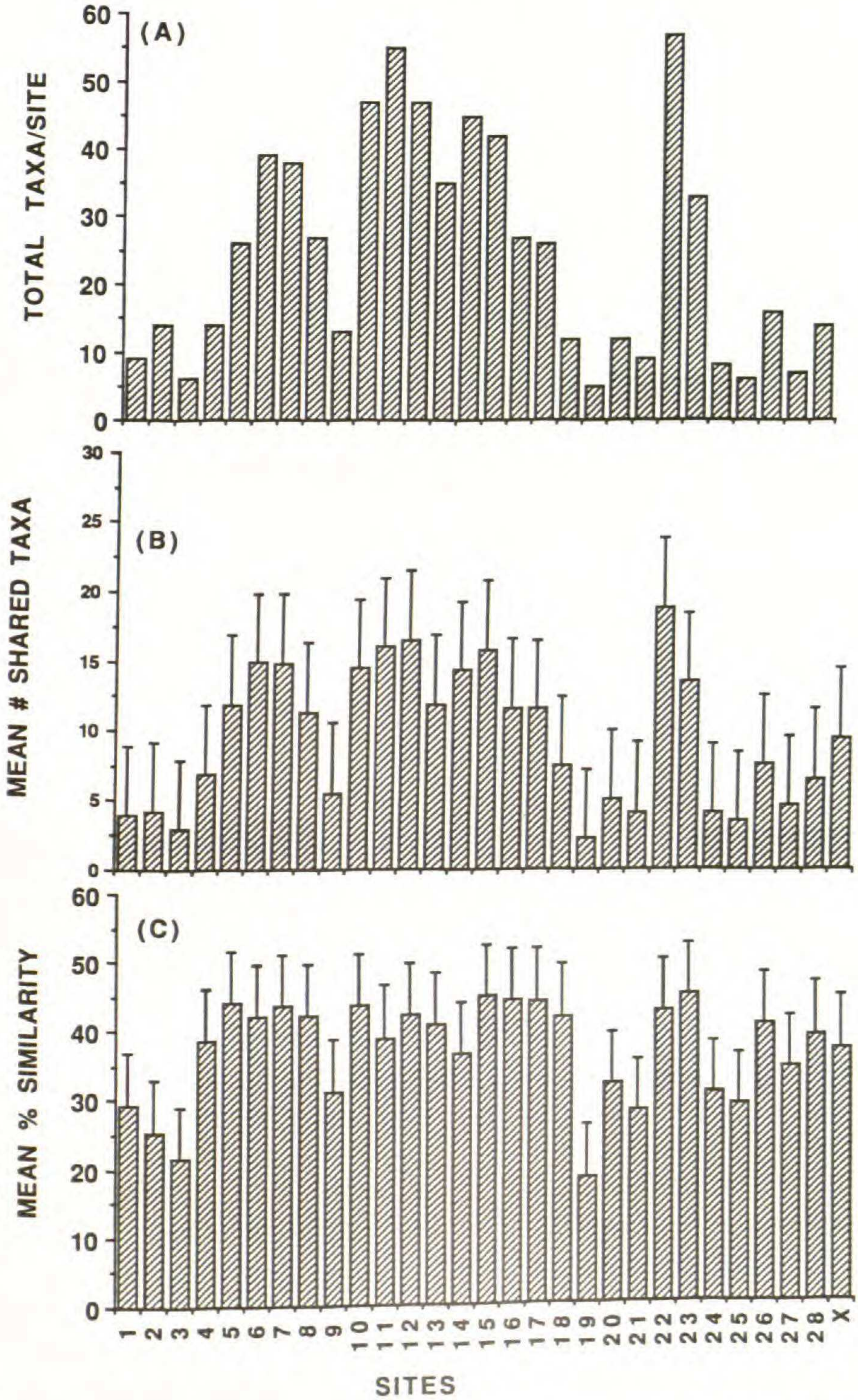

Figure 4. A comparison of the seaweed floras from 28 study sites on Mount Desert Island, expressed as total number of taxa (A), the mean (±S. D.) number of shared taxa (B), and mean % (±S. D.) similarity per site (C). x = mean of all sites.

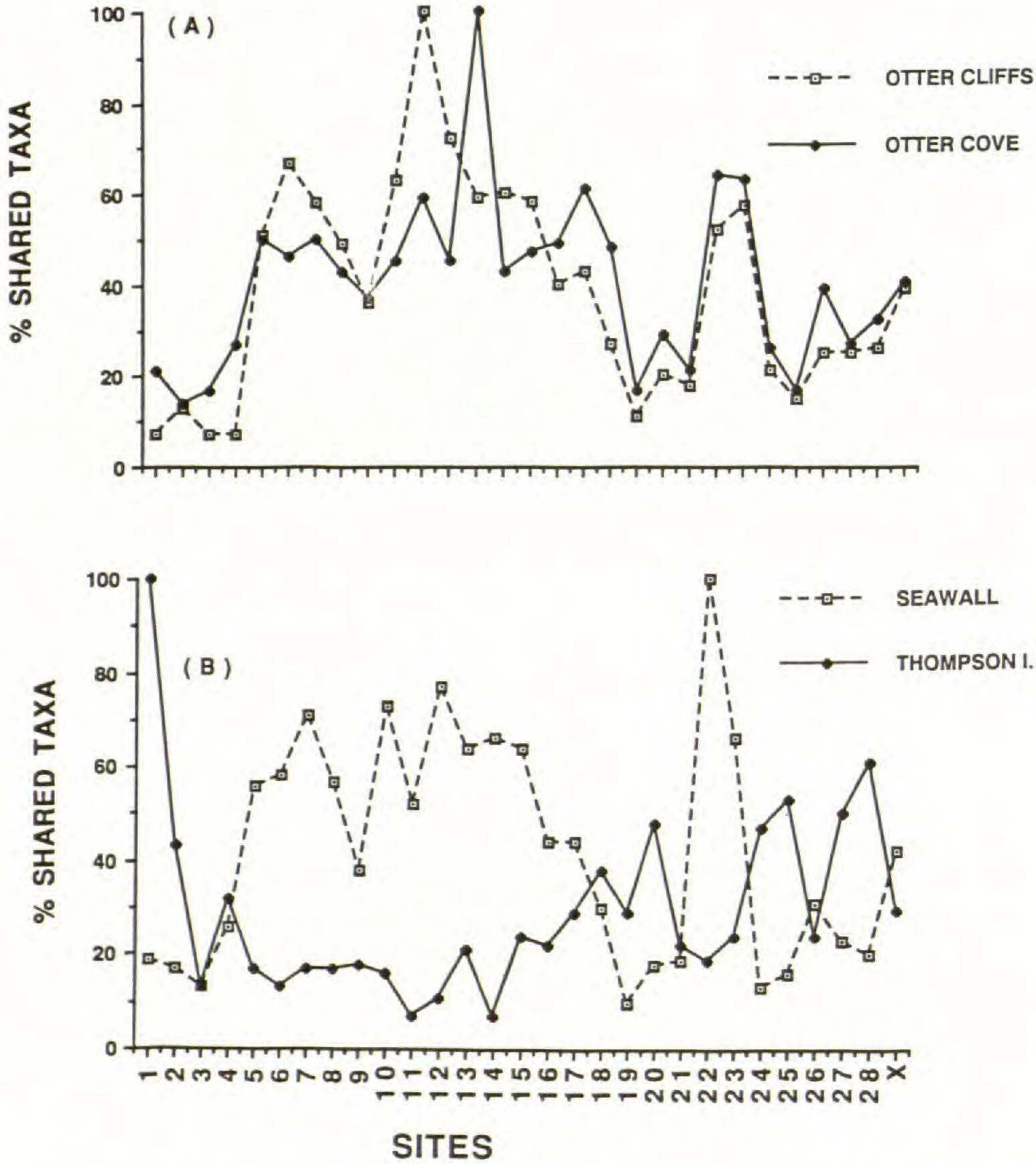

Figure 5. Floristic similarities of four study sites on Mount Desert Island, Otter Cliffs and Otter Cove (A) and Seawall and Thompson Island (B), expressed as the percentage of shared taxa with each of the other 27 study sites. x = mean of all sites.

Zonation studies. The vertical distribution of seaweeds and selected invertebrates at Otter Cliffs, Otter Cove, and Thompson Island (Figure 2, 3; Table 2) was documented during the summer and fall of 1996, 74 years after the initiation of Johnson and Skutch's (1928a, b, c) classical studies at Otter Cliffs (Figure 3A). Before beginning our zonation studies, their original benchmark, which was established in 1923, was re-located; it is embedded within an exposed outer rock at +5.7 m above MLW (Figure 3A,

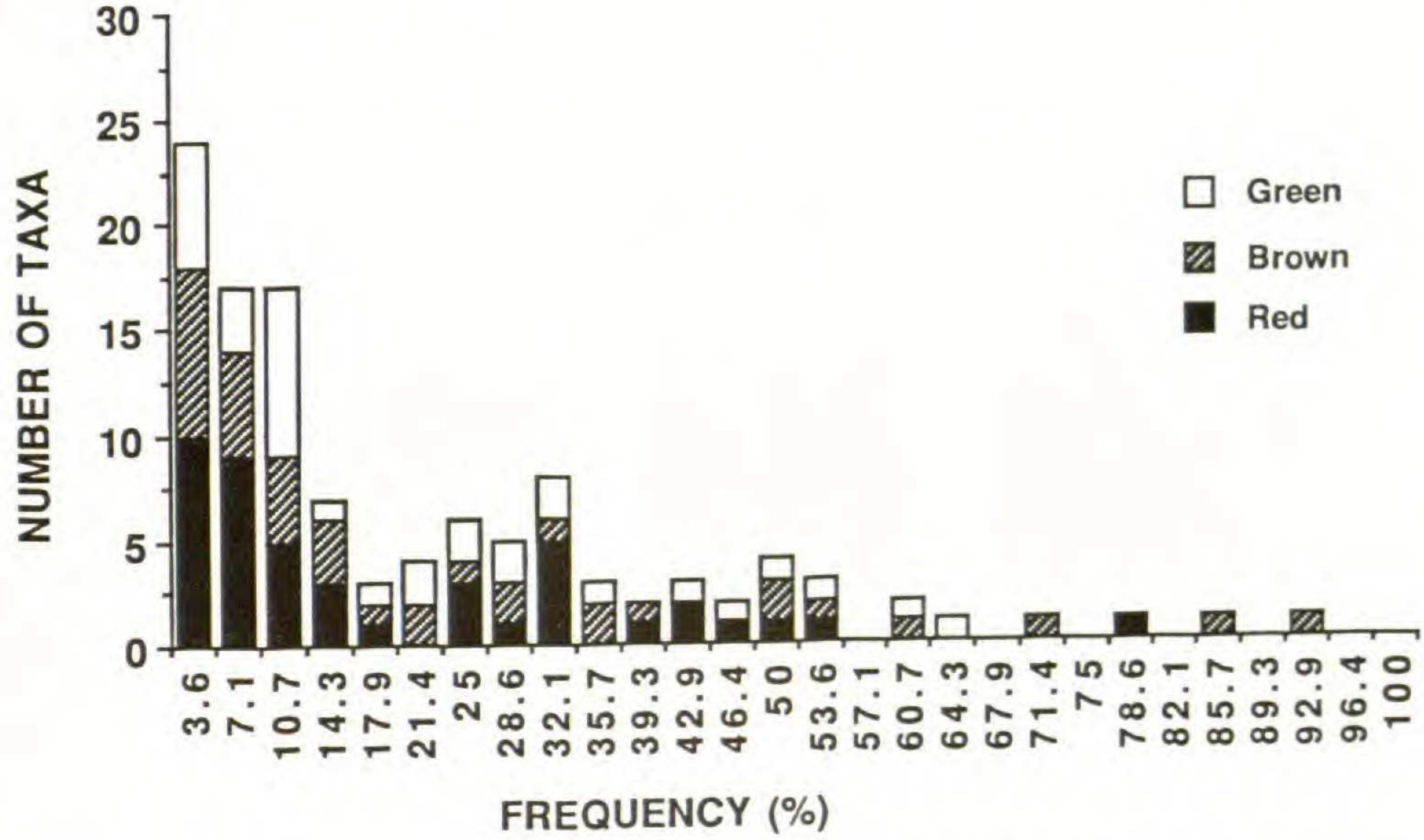

Figure 6. Frequency distribution pattern of 113 Mount Desert Island taxa recorded from 28 present study sites. Taxa found at only one site (3.6% occurrence) are represented by the left-most bar of the graph; those at two sites by the next bar (7.1%), etc.

arrow). Present elevation measurements were related to their datum point, with its height being confirmed after making multiple measurements (plumbing) from the surface to the predicted low tide of that day. A line level and stadia rod were used to make height measurements by pulling a "leveled" line from the benchmark or from secondary reference points. Accuracy of the present elevational measurements is estimated to be ± 5.0 cm. Upper and lower limits of all conspicuous algae are recorded, as well as those for selected invertebrates (e.g., *Semibalanus balanoides*). Some seaweeds were collected for critical identifications in the laboratory. Similar field procedures were used to characterize the biological zones at two other Mount Desert sites (Otter Cove and Thompson Island; Figure 3B, C), while published records from an exposed site in southern Maine (Bald Head Cliff, York) and a semi-exposed site in New Hampshire (Jaffrey Point, Newcastle) were also compared (Femino and Mathieson 1980; Mathieson et al. 1981).

Otter Cliffs (44° 18.58′ N, 68° 11.44′ W), the most exposed of the three Mount Desert zonation sites, is located on the eastern side of Otter Point, approximately 50 km from the Bay of Fundy.

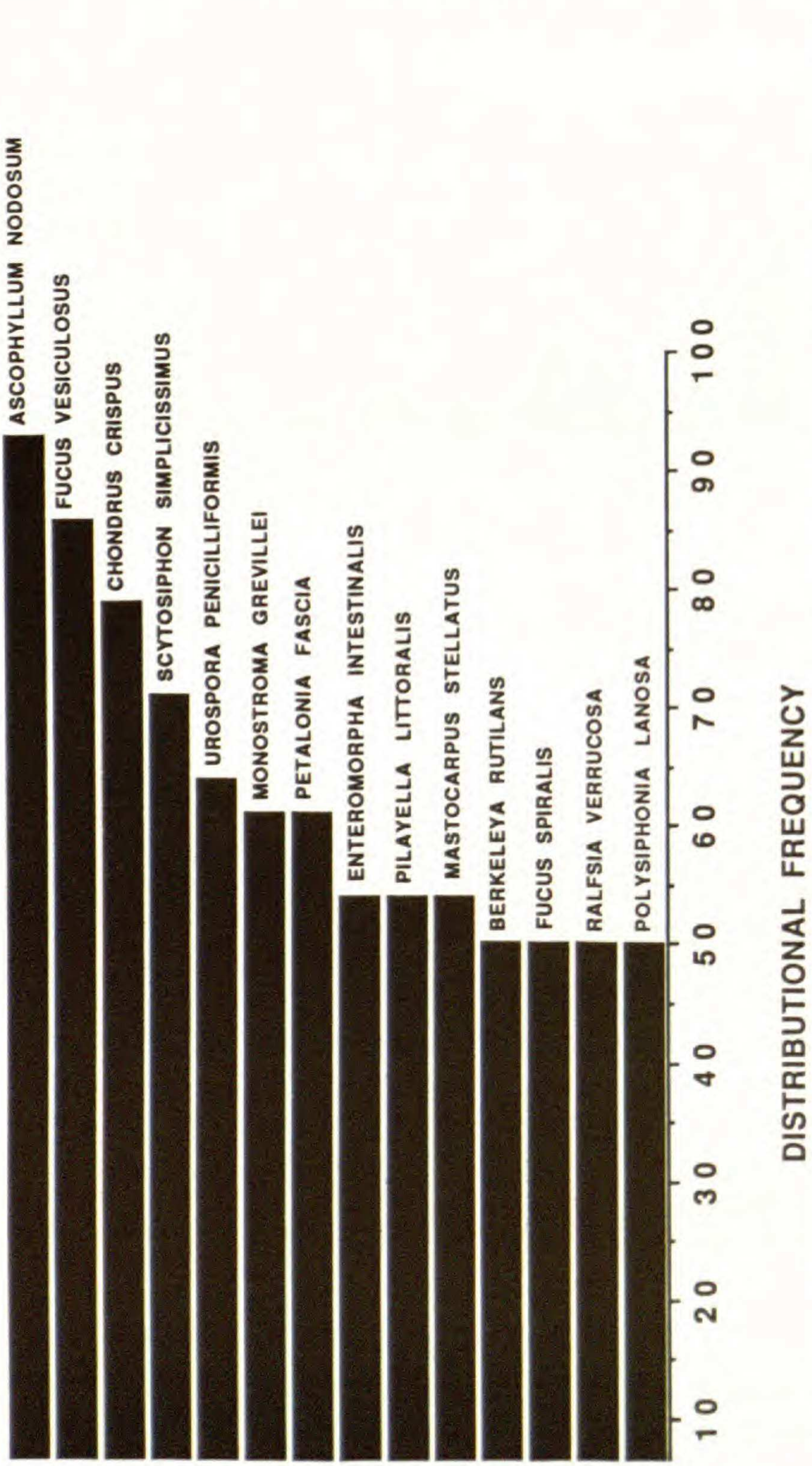

Figure 7. Distributional frequency (%) of the thirteen most common seaweed taxa, plus the benthic colonial diatom *Berkeleya rutilans*, at the 28 present study sites.

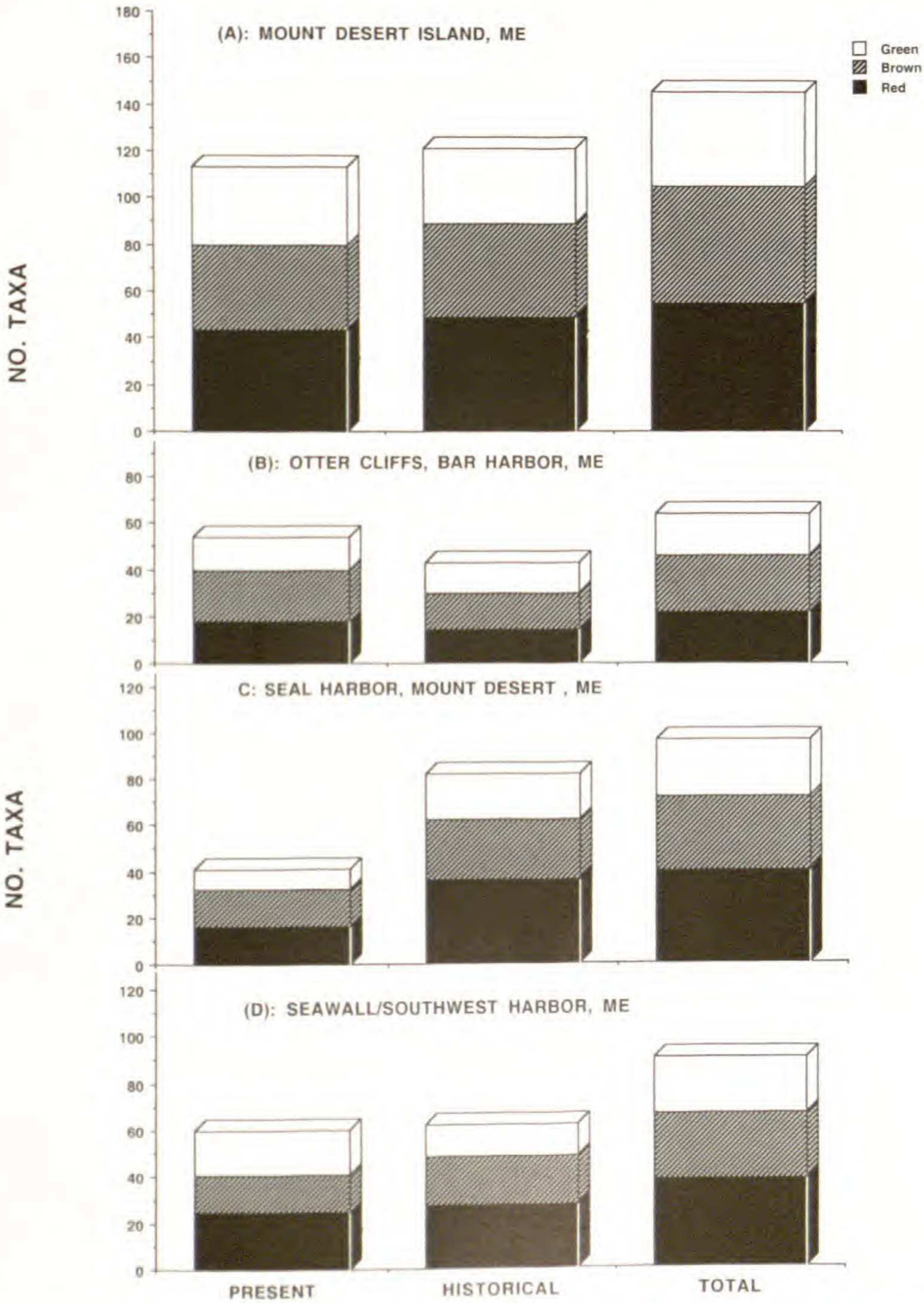

Figure 8. A comparison of present, historical, and combined total seaweed taxa (green, brown, and red) from 28 Mount Desert Island sites (A) and an analogous comparison for three sites: Otter Cliffs (B), Seal Harbor (C), and the Seawall-Southwest Harbor area (D).

Table 2. Zonation comparisons (m above or below MLW) at seven sites in Maine and New Hampshire. Key to symbols: (1) Otter Cliffs, ME—exposed & semi-exposed (Johnson & Skutch, 1928a, b, c); (2) Otter Cliffs, ME—exposed outcrop (1996); (3) Otter Cliffs, ME—semi-exposed site (1996); (4) Otter Cove, ME—sheltered (1996); (5) Thompson I., ME—sheltered (1996); (6) Bald Head Cliff, ME—exposed (1980); (7) Jaffrey Point, NH—semi-exposed (1981); () = tide pool; (−) = subtidal; * = five intertidal species of *Verrucaria* are recorded from this area, with the dominant taxon being *V. striatula* Wahlenberg.

	1	2	3	4	5	6	7
CHLOROPHYCEAE							
Acrochaete viridis (Reinke) (R. Nielsen)							0.0–0.6
Blidingia minima	(1.9) 3.7–5.0		1.8–4.0	3.0–3.2			
Capsosiphon fulvescens							2.2–2.7
Chaetomorpha brachygona							0.0–0.6
Chaetomorpha linum							0.0–0.6
Chaetomorpha melagonium			(1.2)				(−0.2)
Chaetomorpha picquotiana							0.0–0.6
Chlorochytrium cohnii Wright							2.0
Cladophora sericea	(1.2)		(1.2)–1.8 (2.1)				2.2–2.7
"*Codiolum petrocelidis*"							0.3
"*Codiolum pusillum*"	1.7–4.5		2.4–4.0	2.6–3.0			2.0–3.4
Enteromorpha clathrata							2.2–2.7
Enteromorpha compressa	0.9–4.3						
Enteromorpha flexuosa ssp. *paradoxa*							2.2–2.7
Enteromorpha intestinalis	(1.2)		(1.2) 1.5–2.9	3.2		1.8–2.8 (4.7)	2.2–2.7
Enteromorpha linza							0.0–0.5
Enteromorpha prolifera							2.2–2.7

Table 2. Continued.

	1	2	3	4	5	6	7
Enteromorpha torta							2.2–2.7
Epicladia flustrae							0.0–2.2
Monostroma grevillei	2.1–4.3					1.3–2.3	0.0–1.7
Mougeotia sp.	4.3–9.2						
Percursaria percursa							2.2–2.7
Prasiola stipitata		5.4–5.7					2.7–3.3
Protomonostroma undulatum							
f. *pulchrum*						1.0–1.8	0.0–0.9
Rhizoclonium riparium							2.2–2.7
Rhizoclonium tortuosum	0.6–2.1		(1.2)–(3.4)	(1.0)–(1.8)		1.8–2.2	0.0–0.6
Spongomorpha arcta	0.6–2.5 (3.4)		0.1–0.5 (2.1)			0.0–1.9	0.0–0.2
Spongomorpha spinescens	0.0–2.1 (2.7)		0.1–0.5			0.0–(1.8)	0.0
Ulothrix flacca	(1.2) 3.1–4.3						0.8–2.8
Ulothrix speciosa						1.8–3.0	2.5–2.8
Ulva lactuca	0.0–0.9	(3.0)	0.0–1.8 (3.4)	0.0–(1.0)		0.0–1.8	0.0
Ulvaria obscura		0.0–1.0 (3.0)	0.0–0.4 (3.4)			1.3–1.6 (1.8)	0.0–0.5
Urospora penicilliformis	0.6–5.0		2.4–4.0	2.4–3.1		1.8–3.0	1.3–2.5
Urospora wormskjoldii						1.8–3.0	
PHAEOPHYCEAE							
Agarum clathratum	(1.2)			−0.6–(0.4)			0.0–0.2
Alaria esculenta	0.0–0.6 (0.8)	0.0–0.7	0.0 (2.1)			0.0–0.9 (1.8)	0.0
Ascophyllum nodosum	0.6–2.7 (3.5)	(3.5)	0.6–2.8 (3.4)	0.2–2.0	0.2–2.9	1.4–2.3	0.0–2.0
Ascophyllum nodosum							
ecad *scorpioides*					2.0–2.5		
Chordaria flagelliformis	0.5–2.1		(2.0)–(3.4)				0.0–0.1
Dictyosiphon foeniculaceus			(2.0)				0.0

Table 2. Continued.

	1	2	3	4	5	6	7
Ectocarpus siliculosus							0.0
Elachista chondrii			0.1				
Elachista fucicola	0.6–2.5	0.3	0.1–1.5 (3.4)	0.5–2.0			0.0–2.0
Fucus distichus ssp. *distichus*	2.1–4.3	(3.4)–(3.5)	(3.4)			1.2–1.8	0.9–2.2
Fucus distichus ssp. *edentatus*	0.6–2.5	0.3–2.0	0.1 (1.2)				0.0–0.5
Fucus distichus ssp. *evanescens*			0.0–0.6 (2.1)	0.0–(0.4)			0.0–0.5
Fucus spiralis			2.8–4.3	1.9–2.8	2.4–3.5		2.3–2.7
Fucus vesiculosus	1.5–4.5		0.1–3.0	0.0–2.0	0.0–0.8	0.0–1.8	0.0–2.3
Fucus vesiculosus f. *limicola*					2.0–2.5		
Laminaria digitata	0.0–0.5		0.0–(1.2)				0.0–0.1
Laminaria saccharina	(0.8)		0.0–(2.1)	0.0–(0.4)			0.0–0.1
Laminariocolax tomentosoides (Farlow) Kylin							0.0
Leathesia difformis	(1.9)		(1.2)			1.7–2.0	0.0–0.5
Myrionema corunnae							0.0
Petalonia fascia	0.0–1.5 (3.2)			(1.0)–(1.2)		1.5–2.0	0.3–2.2
Petalonia zosterifolia (Reinke) Kuntze							0.0
Pilayella littoralis	0.0–1.5		(1.7)–(2.1)	0.5–1.0 (1.6)			0.0–1.3
Pseudolithoderma extensum				0.0–(1.8)			0.0
"*Ralfsia clavata*"		(3.5)					0.0–0.4
Ralfsia verrucosa	0.6–4.3		(1.2)–(3.5)		−0.2	1.7–2.2 (4.8)	0.0–2.2
Saccorhiza dermatodea	0.0–0.3 (0.8)						0.0–0.1
Scytosiphon simplicissimus			(1.7)–(2.0)	(0.4)–(1.8)			0.3–2.7
Sphacelaria cirrosa			0.4–(2.0)				0.2–1.4

Table 2. Continued.

	1	2	3	4	5	6	7
Ulonema rhizophorum Foslie							0.0–2.5
RHODOPHYCEAE							
Ahnfeltia plicata		0.0–(3.0)	(1.2)				0.0–0.6
Antithamnionella floccosa	(0.6)					(−0.2)–(1.8)	0.0
Audouinella membranacea							0.0–2.0
Audouinella purpurea			(2.0)				0.0–1.3
Audouinella secundata							0.0–1.9
Bangia atropurpurea	1.4–4.1					1.8–3.0	0.6–2.8
Bonnemaisonia hamifera Hariot							0.0
Callocolax neglectus F. Schmitz ex Batters							0.0
Callophyllis cristata							0.0
Ceramium deslongchampii							0.0–0.3
Ceramium nodulosum	(3.4)		0.0–(3.4)			0.0–1.8	0.0–0.5
Ceratocolax hartzii Rosenvinge							0.0
Chondrus crispus	0.0–0.8 (2.7)	0.0–(3.0)	0.0–0.9 (3.4)	0.0–(1.8)		0.0–2.2 (4.8)	0.0–2.1
Choreocolax polysiphoniae Reinsch							0.2–2.0
Clathromorphum circumscriptum	0.0–0.6 (3.4)	0.0–1.0 (3.0)	0.0–(2.6)	0.0–(1.8)		0.0–(1.8)	0.0–2.8
Coccotylus truncatus (Pallas) M. J. Wynne et J. M. Heine							0.0
Corallina officinalis	(3.4)		0.0–(3.4)	0.0–(1.8)			0.0–0.1
Cystoclonium purpureum							0.0–0.2
Devaleraea ramentacea	0.0–0.8 (3.4)	0.0–1.0 (3.0)	0.0–0.4 (3.4)			0.0–1.0 (1.8)	0.0–0.1
Dumontia contorta				(0.4)–(1.8)	0.0–0.2		0.0–2.5

Table 2. Continued.

	1	2	3	4	5	6	7
Erythrodermis traillii (Holmes ex Batters) Guiry et Garbary							0.0
Erythrotrichia carnea				0.0–(2.1)			0.0–0.6
Gymnogongrus crenulatus							0.0
Hildenbrandia rubra		(3.5)	0.0–(3.5)	0.0–0.5 (1.6)	0.0–0.2	0.0–2.2 (4.8)	0.0–0.6
Lithothamnion glaciale							0.0–0.4
Mastocarpus stellatus	2.5	0.0–0.7	0.0–2.0	0.1–(1.2)		0.0–2.2	0.0–2.5
Palmaria palmata	0.0–2.5	0.0–0.8 (1.0)	0.0–1.5 (2.1)			1.6–1.8	0.0–0.1
"*Petrocelis cruenta*"		0.0–1.0	0.0–0.4 (2.1)	0.0–(1.8)		0.0–1.8	0.0–0.3
Peyssonnelia rosenvingii							0.0–0.3
Phycodrys rubens							0.0–0.2
Phyllophora pseudoceranoides							0.0
Phymatolithon foecundum (Kjellman) Düwel et Wegeberg							0.0
Phymatolithon lenormandii							0.0–0.3
Phymatolithon tenue							0.0
Plumaria plumosa							0.0–1.3
Pneophyllum fragile Kützing							0.0
Polysiphonia elongata							0.0
Polysiphonia flexicaulis				0.0–(2.1)	0.0–0.2		0.0
Polysiphonia lanosa	1.8–3.0		0.6–2.5	0.0–1.2			0.0–2.0
Polysiphonia nigra (Hudson) Batters							0.0
Polysiphonia stricta	0.0–2.5	0.0–1.0					0.0–0.4
Porphyra leucosticta	2.1						0.0–2.4
Porphyra miniata							0.0–0.2
Porphyra umbilicalis	0.6–3.5	0.8–1.4	0.0–3.0				0.0–2.5

Table 2. Continued.

	1	2	3	4	5	6	7
Porphyridium purpureum (Bory) Drew et Ross	4.3–9.2						
Rhodomela confervoides			0.0–(1.2)				0.0–0.3
Titanoderma corallinae							0.0–0.1
Titanoderma pustulatum							0.0–0.5
BACILLARIOPHYCEAE							
Berkeleya rutilans			(1.2)	(0.4)–(1.2)			
CYANOPHYCEAE							
Calothrix fasciculata	4.3–9.2						
Calothrix scopulorum	2.1–4.9						
Oscillatoria sp.	4.3–9.2						
LICHENS							
Verrucaria spp.*	2.1–4.3		3.5–6.3	0.5–6.5	0.0–4.0		
SPERMATOPHYTA							
Zostera marina				(1.4)			
ANIMALS							
Mytilus edulis		0.3–1.0 (3.5)	0.8–(3.5)	0.0–(1.8)		0.0–3.0	
Semibalanus balanoides		0.3–3.8 (4.4)	0.0–3.5	1.3–2.8	0.7–3.2	1.5–3.4	0.1–2.7
Serpulid				(1.4)			
Strongylocentrotus droebachiensis			(1.2)–(2.0)	0.0–(1.4)			

Its granitic outcrops, which are the highest ocean cliffs on the U. S. Atlantic coast (Butcher 1987), jut directly south into the North Atlantic, exposing it to extreme northeastern storms and waves that reach or exceed 6 m (Figure 3A). Two distinct habitats are evident: a highly exposed cluster of outer rocks that is accessible only at extremely low tides and a nearby semi-exposed vertical cliff. Johnson and Skutch (1928a, b, c) presented composite data for the site. Otter Cliffs and Otter Cove (Figure 3B) have an identical tidal amplitude (4.6 m). Otter Cove (44° 18.79′ N, 68° 11.89′ W) is a moderately protected open coastal habitat about 0.5 km west of Otter Cliffs, on the opposite side of Otter Point (Figure 2). Its granitic outcrops have a more horizontal contour than those at Otter Cliffs. Thompson Island (44° 25.58′ N, 68° 22.07′ W), located 20 km northwest of Otter Cliffs, is a protected two-hectare island within Mount Desert Narrows (Figure 2). It has a greater tidal amplitude than the other two sites (approximately 5 m); its substratum consists of pebbles, sand, and mud scattered amongst a few granitic outcrops. There is also a restricted fringing marsh (Figure 3c).

HABITAT DESCRIPTION AND HISTORY

Mount Desert Island, which is located northeast of Penobscot Bay (Figure 1), is the third largest insular environment on the East Coast of the United States and the largest in Maine (Platt 1996; Simpson 1987). It covers approximately 173 km^2 (ca. 26,058 ha), has a perimeter of about 64,390 km, and maximum length and width of 24 and 19 km, respectively. The Cranberry Isles, plus Swans and Long Islands, all lie to the south and southwest of Mount Desert (Figure 1, 2). Biologically, Mount Desert is situated near the boundary of the Boreal (Canadian) and Austral regions and contains a mixture of northern and southern species (Anonymous 1991, 1992; Butcher 1987; Moore 1921; Proctor 1927, 1938, 1946; Rand and Redfield 1894; Simpson 1987).

The island's coastline is composed primarily of granitic rock, with many shorelines consisting of sloping ledges of crystalline granite made up of quartz, feldspar, and other minerals (Butcher 1987). The island's diverse and irregular coastline ranges from exposed and semi-exposed open coastal sites, to hectares of protected waters, extensive mudflats, and salt marshes. The south shore between Schooner Head and East Point (including Otter

Cliffs), plus the area from Seawall to Bass Harbor Head, is most exposed to the open Atlantic (Figure 2; Appendix). Protected open coastal habitats are interspersed among the exposed ones, particularly within the embayed waters behind the Cranberry Isles, Somes Sound, Seal Harbor, Northeast Harbor, Southwest Harbor, and Manset Harbor (Proctor 1927; Rand and Redfield 1894).

Somes Sound (Figure 2) is a unique site topographically and historically. It is a long, sheltered arm located within the center of the island (approximately 8 km), dividing the island into two major peninsulas. Geologically, it represents a narrow, glacially carved trough that extends north to south, roughly parallel to the Pleistocene ice advance in this area (Butcher 1987; Johnson 1925). Because of its pronounced topographic coastal relief, which may reach 250 m above sea level, it has been referred to as the only fjord on the east coast of the United States (Chapman 1970; Condon 1994; Johnson 1925, 1987); however, its low fresh-water input and lack of stratification are typical of other shallow Maine estuaries (McAlice 1977; Pettigrew et al. 1997). Summer surface water temperatures and salinities in Somes Sound, which are typical for the island as a whole, vary from 13.0–14.5°C and 31.7–31.9 ppt between the mouth and head, while spring temperatures are lower and salinities are not appreciably reduced (Ketchum and Cass 1986).

A shallow strait in the northwest part of the island, Mount Desert Narrows, connects the nearby Eastern and Western Bays that in turn merge with Blue Hill and Frenchman Bays (Figure 2). Two bridges connect Thompson Island to the mainland on the north and Mount Desert to the south. The open waters of Frenchman Bay on the eastern side of the island contain many small islands, which, along with Mount Desert, enclose a large body of water between them and the mainland to the north (Proctor 1927). Several rivers flow into Frenchman Bay, including the Jordan and Skillings. Some drain the adjacent terrain, while others are tortuous channels with swift currents due to tides with vertical ranges of 4.0 to 5.0 m. Frenchman Bay is different from the exposed waters to the south and Blue Hill Bay to the west. The latter is a sheltered and often muddy location fed by several large brooks and the Union River.

Mount Desert Island has long been a destination for explorers, travelers, and tourists (Morrison 1960, 1972; Simpson 1987).

Shell heaps testify to the presence of native American encampments dating back 6,000 years (Anonymous 1991, 1992; Butcher 1987; Condon 1994). The French explorer Samuel de Champlain provided the first positive description of Mount Desert in 1604 and correctly identified it as an island (Duncan et al. 1995; Simpson 1987). Champlain was so impressed with the bleak and barren grandeur of the glacially scoured mountains (Belknap et al. 1986; Butcher 1987; Kjerfve 1989) that he called it "Isles des Monts Desert" (Johnson 1987). The rise of Mount Desert as a resort destination occurred in the late 1800s, after such artists as Thomas Cole and Frederick Church began summering in Bar Harbor (Anonymous 1987, 1991, 1992; Butcher 1987; Simpson 1987; Tree and Roundy 1995). Naturalists, including John James Audubon and Louis Agassiz, found the island attractive because of its wide diversity of organisms, as well as its nearness to the boundary line between two ornithological and botanical zones (Simpson 1987).

The legislative history of Acadia National Park, which now comprises 12,950 hectares of Mount Desert Island (ca. 50%), officially began with the establishment of Sieur de Monts National Monument in 1916 (Anonymous 1991, 1992). The name was changed to Lafayette National Park in 1919 and ultimately to Acadia in 1929. An additional 13 km^2 (ca. 2,023 ha) of Acadia includes Isle au Haut (High Island) to the south and some parts of the Schoodic Peninsula to the north (Figure 1). Acadia is the only national park in the northeastern United States and is visited by several million people each year (>4.5 million in 1990). Overall, its popularity is second only to Yellowstone National Park and there is concern that anthropogenic impacts such as traffic and deteriorating air quality may cause irreparable damage within the park (Anonymous 1992, 1995; Eckert et al. 1994, 1997). Greene et al. (1992) emphasize the significance of historical resource inventories in evaluating possible environmental damage. The studies of benthic marine plants reported here are intended to supplement such historical inventories and contribute to the long-term monitoring of Acadia National Park and Mount Desert Island.

RESULTS

Present-day floristic patterns. A total of 113 seaweeds is recorded from the 28 present study sites, including 33 Chlorophyceae, 37 Phaeophyceae, and 43 Rhodophyceae (Table 1). In addition, the benthic colonial diatom *Berkeleya rutilans* (Bacillariophyceae) is conspicuously evident. The pattern of species richness per site is highly variable (Figure 4A), presumably due to pronounced habitat variability (see previous and next sections). The highest numbers of taxa and percentages of the total flora are found on the exposed open coast at Otter Cliffs (54 and 48%) and Seawall (60 and 53%); the lowest numbers are recorded at several sheltered sites, including Hadley Point (7 and 6.2%) Somesville (6 and 5.3%), Seal Cove (6 and 5.3%), and Bartlett Narrows (6 and 5.3%). The mean number of taxa per site is relatively low (24.5 ± 16.2): green algae 7.0 ± 5.0, brown algae 9.0 ± 4.9, and red algae 8.1 ± 7.1.

As shown in Figure 4B, the pattern of mean number of shared taxa "mimics" species richness, while the values for mean percent similarity exhibit a broader, more uniform pattern (Figure 4C). The overall mean richness values for the 28 present sites are relatively low, being 9.5 ± 5.1 taxa and 36.8 ± 7.6%. Seawall, the site with the highest number of taxa (60), has the highest number of shared taxa (19.0 ± 14.4) and a relatively high percent similarity pattern of 42.0 ± 24.6%. Otter Cliffs, the next most diverse site (54 taxa), has a lower number of shared taxa (15.5 ± 12.7) and percent similarity (39.0 ± 24.0%). By contrast, the four sites with the most reduced floras exhibit the following patterns: (1) Bartlett Narrows, 6 taxa, 4.6 ± 1.7 shared taxa, and 34.0 ± 18.2% similarity; (2) Hadley Point, 7 taxa, 3.0 ± 2.1 shared, and 21.5 ± 20.3% similarity; (3) Seal Cove, 6 taxa, 3.5 ± 1.2 shared, and 28.6 ± 19.3% similarity; and (4) Somesville, 6 taxa, 2.2 ± 1.2 shared, and 18.3 ± 17.6% similarity.

A further comparison of floristic similarities at Otter Cliffs (site 11), Otter Cove (site 13), Seawall (site 22), and Thompson Island (site 1) is given in Figure 5. The values are expressed as percentage of shared taxa with each of the other 27 study sites. Three of these sites were chosen because of concurrent zonation studies (see below), while the fourth (Seawall) had the most diverse flora (Figure 4A). Recalling the clockwise orientation of the sites starting from Thompson Island (Figure 2), the floristic affinities of the exposed site at Seawall show the following spatial pattern: (1) moderately high similarities (66%) with nearby Bass Harbor Head Light (site 23); (2) low-moderate similarities (13–31%) between Bass Harbor (site 24) and Hulls Cove (site 4); (3) maximum affinities with Great Head (site 7, 71%), Thunder Hole (site 10, 73%), and Otter Point (site 12, 77%); and (4) lowest overall similarities with Somesville (site 19, 10%). By contrast, Otter Cliffs has its maximum similarities to nearby Schooner Head (site 6, 67%), Thunder Hole (site 10, 63%), and Otter Point (site 12, 72%), and its lowest affinities with Somesville (site 19, 11%) and those sites between Thompson Island and Hulls Cove (sites 1–4, 7–13%). Otter Cove's affinities are analogous to Otter Cliffs, except for its greater similarities between sites 1–4 (Thompson Island to Hulls Cove, 14–27%) and sites 16–28 (Bracy Cove to Indian Point, 17–64%). Thompson Island shows a very skewed pattern, with maximum affinities at sites 20 (Somesville at Rt. 102, 48%), 25 (Seal Cove, 53%), and 28 (Indian Point, 61%).

Figure 6 outlines the frequency distribution patterns of the 113 individual taxa recorded from the 28 present study sites on Mount Desert Island. Twenty-three species (5 green, 8 brown, and 10 red algae) are restricted to a single site (3.6% occurrence), while 34 others (10 green, 9 brown, and 15 red algae) occur at two or three sites (7.1–10.7% occurrence). Only three taxa occurred at >21 of the 28 sites (Figure 7; Table 1), namely, *Ascophyllum nodosum* (93%), *Fucus vesiculosus* (86%), and *Chondrus crispus* (79%). The other common species are *Scytosiphon simplicissimus* (71%), *Urospora penicilliformis* (64%), *Monostroma grevillei* (61%), *Petalonia fascia* (61%), *Enteromorpha intestinalis* (54%), *Pilayella littoralis* (54%), *Mastocarpus stellatus* (54%), *Berkeleya rutilans* (50%), *Fucus spiralis* (50%), *Ralfsia verrucosa* (50%), and *Polysiphonia lanosa* (50%).

Historical floristic comparisons. As shown in Figure 8A, 121 seaweeds have been previously recorded for Mount Desert (49 Rhodophyceae, 40 Phaeophyceae, and 32 Chlorophyceae) compared with 113 taxa from recent sampling, i.e., 43 Rhodophyceae, 37 Phaeophyceae, and 33 Chlorophyceae. This represents a total of 146 taxa when the two lists are combined, including 41 Chlorophyceae, 50 Phaeophyceae, and 55 Rhodophyceae. In addition, a common diatom *Berkeleya rutilans* is listed in Table 1. Eighty-eight of these taxa are found in both historical and present collections (i.e., 37 red, 27 brown, and 24 green algae). Thus, a comparison of Mount Desert's total flora shows an approximate equality of species numbers (121 vs. 113) and a relatively high percent similarity (75.2%). Similar comparisons of three individual sites (Figure 8B–D) show the following patterns: (1) Otter Cliffs, 54 current taxa, 43 historical, 64 combined total, and a 68% similarity; (2) Seal Harbor, 41 current taxa, 82 historical, 97 combined total, and a 43% similarity; and (3) the Seawall-Southwest Harbor area, 60 current taxa, 63 historical, 90 combined total, and a 54% similarity.

Present-day zonation patterns. As shown in Figure 9 and Table 2, several conspicuous differences in zonation patterns are evident when the Mount Desert sites of Otter Cliffs, Otter Cove, and Thompson Island are compared with previously published records. The biological zones at Otter Cliffs (Figure 3A) are the most expansive (>5.7 m) due to extreme wave exposure, followed by the exposed Bald Head Cliff site (4.8 m), the semi-exposed Jaffrey Point (3.4 m), and the more sheltered Otter Cove (3.2 m) and Thompson Island sites (3.5 m). Thus, the biological zones exceed mean tidal amplitudes at Otter Cliffs (4.6 m), Bald Head Cliff (2.7 m), and Jaffrey Point (2.7 m), while they are less at Otter Cove (4.6 m) and Thompson Island (5.0 m). As shown in Table 2, the freshwater green alga *Mougeotia* and the terrestrial-marine red alga *Porphyridium purpureum* were recorded by Johnson and Skutch (1928c) within the extreme spray-mist zone at Otter Cliffs, extending from 4.3 m–9.2 m (Figure 9A; Table 2); neither of these taxa were found at the other study sites.

Pronounced localized differences in zonation patterns are evident at Otter Cliffs (Figure 9B–D). That is, the exposed outer rocks have a very circumscribed zonation (see below) and a reduced number of species compared with the adjacent semi-exposed cliff. A composite of the two major habitats at Otter Cliffs (Figure 9B) tends to show a more "typical" zonation pattern, similar to Jaffrey Point (Figure 9G), with species richness increasing from top to bottom and a conspicuous stratification of colors. Green algae dominate the upper shoreline, reds are most conspicuous in the lower shore and browns exhibit an intermediate pattern. Many species exhibit disjunct vertical distributions, extending higher within than outside of tide pools (Table 2). A pattern of decreasing species richness with enhanced shelter is also evident on Mount Desert Island, from Otter Cliffs (Figure 9B–D), to Otter Cove (Figure 9E) and Thompson Island (Figure 9F). Of the three groups of seaweeds, the green algae showed the

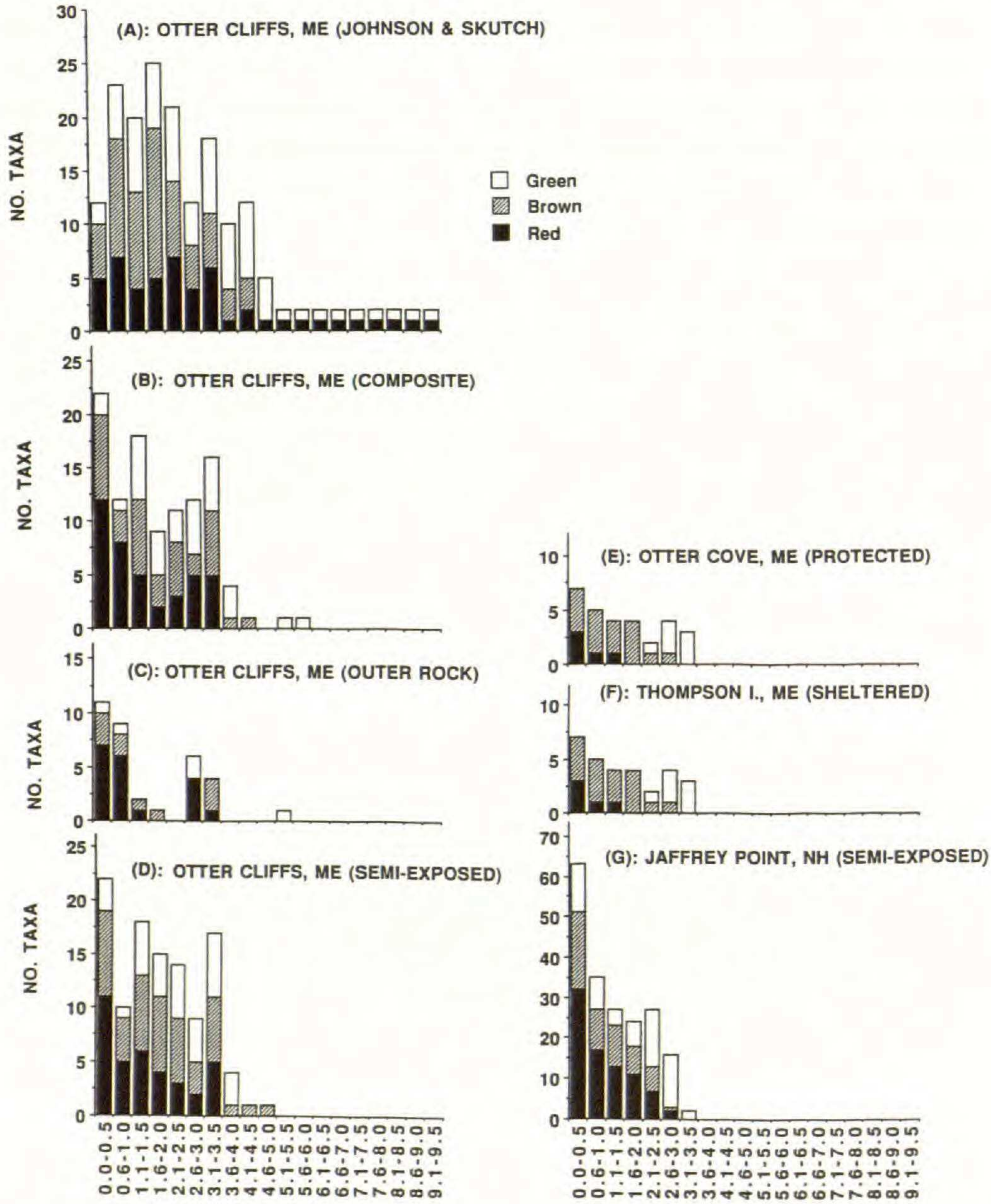

Figure 9. The number of seaweed taxa (green, brown, and red) occurring at 0.5 m intervals from the upper to the lower intertidal zone at six sites in Maine (A–F) and one (G) in New Hampshire: (A) Otter Cliffs (from Johnson and Skutch 1928a); (B) Otter Cliffs, composite of C and D below; (C) Otter Cliffs, outer rocks; (D) Otter Cliffs, inner semi-exposed rocks; (E) Otter Cove, protected open coast; (F) Thompson Island, sheltered bay; (G) Jaffrey Point, semi-exposed open coast.

most conspicuous decrease in species richness (not biomass) with increasing shelter.

A number of unique features are evident when the four major zones (maritime, splash, intertidal, subtidal) on Mount Desert are compared (Table 2). The maritime zone, or the area subjected to salt spray above the highest tides, is absent from the exposed rocks at Otter Cliffs that only reach 5.7 m above MLW. It is well developed, however, on the adjacent cliffs (+9.2 to +15.2 m). Within this zone several lichens (*Caloplaca*, *Leonia*, *Physia*, *Ramilina*, *Verrucaria*, and *Xanthoria*), blue green algae (*Calothrix* and *Oscillatoria*), and seed plants (*Abies balsamea*, *Empetrum nigrum*, *Juniperus horizontalis*, *J. communis* var. *depressa*, *Picea glauca*, and *Plantago oliganthos*) occur. Many seed plants exhibit extensive wind/salt damage. At Otter Cove (Figure 3B) and Thompson Island (Figure 3C) the maritime zone approximates mean tidal limits, extending to +4.6 and +5.0 m, respectively. The two most conspicuous trees at these sites, *A. balsamea* and *P. glauca* show little wind/salt damage. The splash zone, or the area affected by wave action above high tide, exhibits pronounced spatial differences. It extends to the top of the outer rocks at Otter Cliffs (+5.7 m) where only a few localized patches of the guanotrophic green alga *Prasiola stipitata* occur (Table 2). On the adjacent semi-exposed cliff, it extends to about +9.2 m, with the marine lichen *Verrucaria* spp. and various blue green algae (*Calothrix* and *Oscillatoria*) forming extensive greenish-blackish crusts. A splash zone is absent at Otter Cove and Thompson Island, and their biological zones do not exceed ambient tidal extremes (see above).

The intertidal zone, or the region regularly covered and uncovered by tides, can be divided into three major subzones: (1) an upper barnacle zone dominated by *Semibalanus balanoides*; (2) a mid-shore brown algal zone with *Ascophyllum nodosum* and *Fucus* spp.; and (3) a lower red algal zone with *Chondrus crispus* and *Mastocarpus stellatus*. The upper intertidal at the exposed Otter Cliffs rocks (ca. +3.0 to +4.6 m) is dominated by *S. balanoides*, while several disjunct taxa occur within high tide pools (*Ulva lactuca*, *Ulvaria obscura*, *A. nodosum*, *Fucus distichus* ssp. *distichus*, "*Ralfsia clavata*," *Ahnfeltia plicata*, *Chondrus crispus*, *Clathromorphum circumscriptum*, *Devaleraea ramentacea*, *Hildenbrandia rubra*, and *Mytilus edulis*). The mid-intertidal (ca +1.6 to +2.9 m) only has a few stunted plants of *F. distichus* ssp. *edentatus*, plus *S. balanoides*, while the low intertidal (0.0 to ca +1.5 m) contains many of the same disjunct tide pool taxa, in addition to *Alaria esculenta*, *Elachista fucicola*, *M. stellatus*, *Palmaria palmata*, "*Petrocelis cruenta*," *Polysiphonia stricta*, *Porphyra umbilicalis*, *M. edulis* and *S. balanoides*. The semi-exposed habitat at Otter Cliffs contains a greater variety of organisms than the outer highly exposed rocks (Figure 9C, D), with *S. balanoides* dominating the upper shore (to +3.5 m), *A. nodosum* and *F. vesiculosus* the mid-intertidal (to +2.8 m), and several species in the lower intertidal (*C. crispus*, *M. stellatus*, *P. palmata*, *U. lactuca*, and *M. edulis*). The intertidal zone at Otter Cove is primarily dominated by *S. balanoides*, *A. nodosum*, *F. vesiculosus*, *C. crispus*, and *M. edulis*; epiphytic (*Pilayella littoralis*) and hemiparasitic species (*Polysiphonia lanosa*) are abundant. Analogous zones at Thompson Island are readily differentiated, with *Fucus spiralis* extending from +2.4 to +3.5 m, *A. nodosum* from +0.2 to +2.9 m, and *F. vesiculosus* from 0.0 to +0.8 m.

The upper subtidal zone, or fringe region just below mean low water (MLW), shows pronounced differences in species composition and abundance (Table 2). For example, at the exposed Otter Cliffs, this zone is dominated by dense patches of *Semibalanus balanoides* and *Mytilus edulis*; wave-damaged *Alaria esculenta* and many red and green algae are also evident. *Fucus distichus* ssp. *edentatus* marks the upper subtidal zone at the adjacent semi-exposed cliffs. Several kelps (*A. esculenta*, *Laminaria digitata*, and *L. saccharina*), green algae (*Spongomorpha spinescens* and *Ulva lactuca*), and red algae (*Ceramium nodulosum*, *Clathromorphum circumscriptum*, *Devaleraea ramentacea*, and "*Petrocelis cruenta*") are also present. The shallow subtidal at Otter Cove has dense populations of *Mastocarpus stellatus*, *U. lactuca*, and *L. saccharina*, as well as the crustose algae *C. circumscriptum*, "*P. cruenta*," and *Pseudolithoderma extensum*. Somewhat deeper, *Strongylocentrotus droebachiensis* forms extensive "urchin barrens" in which only residual populations of *Agarum clathratum* are evident on a "pavement" of the pink crustose coralline alga *C. circumscriptum*. Thompson Island has a very limited subtidal flora, and most plants (*Dumontia contorta*, *Polysiphonia flexicaulis*, *Hildenbrandia rubra*, and *Ralfsia verrucosa*) occur on scattered granitic boulders and pebbles.

Figure 10 illustrates the upper distributional limits of seven conspicuous seaweeds at five sites on Mount Desert Island (Otter Cliffs: a composite, the exposed outer rocks, and the semi-exposed cliffs; Otter Cove, and Thompson Island), plus Bald Head

Cliff, Maine, and Jaffrey Point, New Hampshire. *Ascophyllum nodosum* shows a fairly uniform distribution, being most circumscribed at Otter Cove and Jaffrey Point. *Fucus vesiculosus* exhibits a conspicuous attrition with enhanced shelter between the Otter Cliffs composite site and Thompson Island and a moderate resurgence at Bald Head and Jaffrey Point. *Mastocarpus stellatus* and *Chondrus crispus* are highly reduced at the most exposed sites, the outer rocks of the highly exposed Otter Cliffs and those of the more protected Otter Cove. The former species has an erratic distribution, while the latter species shows a southerly enhancement. *Clathromorphum circumscriptum* exhibits a more northern pattern than *C. crispus* and is most prevalent in the composite of Otter Cliffs and their highly exposed outer rocks. *Palmaria palmata* is most common at the composite of Otter Cliffs, it dips on the exposed outer rocks, and is lowest at the semi-exposed Jaffrey Point. *Devaleraea ramentacea* is relatively uniform at all sites except at Jaffrey Point, where it is reduced.

The upper and lower distributional limits of *Verrucaria* spp., *Urospora penicilliformis*, and *Blidingia minima* are illustrated in Figure 11. *Verrucaria* shows its maximum upward expansion at the semi-exposed rocks of Otter Cliffs and the more protected coast of Otter Cove with analogous lower distributional limits, except for the latter site and Thompson Island. *Urospora* is most expansive at the composite of Otter Cliffs and shows a clinal decrease/compression at the other five sites. *Blidingia* shows a maximum upper distribution at the same site; minimum limits are seen at Otter Cove and Jaffrey Point. Its lower distribution is somewhat erratic, with maximum and minimum levels in the composite and semi-exposed areas of Otter Cliffs, respectively.

Historical zonation comparisons. The use of Johnson and Skutch's benchmark, which was established in 1923 at Otter Cliffs, has insured that the present elevational measurements are directly comparable. Based upon these comparisons, 13 of the 32 shared taxa (4 green, 4 brown, and 5 red) show a conspicuous reduction (0.5 to 2.0 m) in their upper distributional limit (Table 3). Three species also show a drop in their lower distributional limits: *Blidingia minima* (3.7 m vs. 1.8 m), *Fucus vesiculosus* (1.5 m vs. 0.1 m) and *Porphyra umbilicalis* (0.6 m vs. 0.0 m). None of the 32 shared taxa shows a significant upward expansion of its zone (>0.2 m).

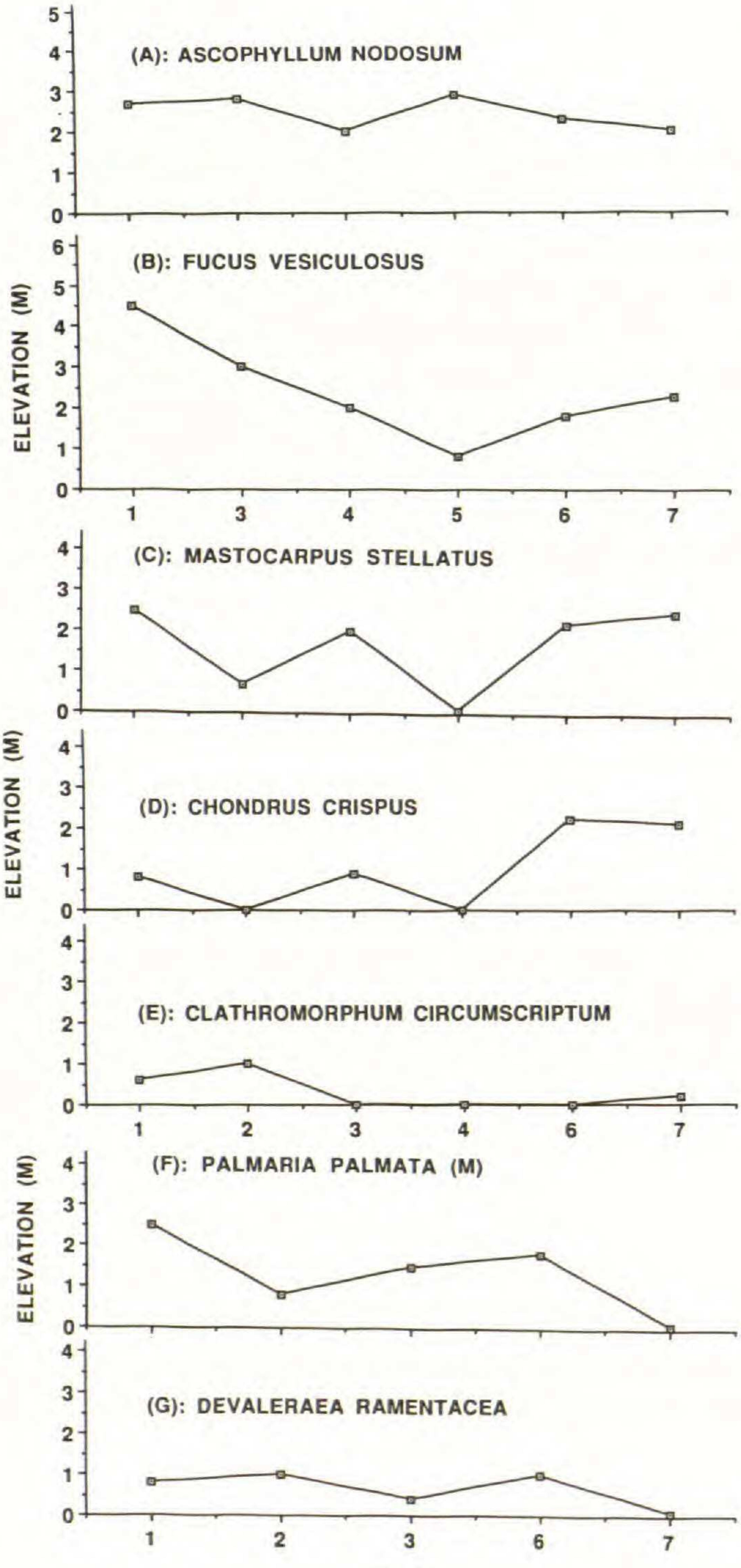

Figure 10. Upper distributional limits of non-tide pool populations of *Ascophyllum nodosum* (A), *Fucus vesiculosus* (B), *Mastocarpus stellatus* (C), *Chondrus crispus* (D), *Clathromorphum circumscriptum* (E), *Palmaria palmata* (F), and *Devaleraea ramentacea* (G) at seven sites. The sites are: (1) Otter Cliffs (from Johnson and Skutch 1928a); (2) outer rocks at Otter Cliffs;

DISCUSSION

Based upon historical and recent collections, the macroalgal flora on Mount Desert Island, Maine, is composed of 145 taxa, which exceeds insular floras within nearby Penobscot Bay and at other northwest Atlantic sites (Mathieson and Penniman 1986; Mathieson et al. 1996). When comparing historical and recent collections at three individual sites on Mount Desert, the lowest percent similarity occurred at Seal Harbor, an embayment having intense human activity, while other sites showed only small changes. Zonation studies revealed altered vertical patterns and a reduction in species diversity with increasing exposure, with these patterns being similar to those reported for the Bay of Fundy (Morton 1991) and rocky shores in general (Dawes 1998; Lewis 1964; Lobban and Harrison 1994; Lüning 1990; Stephenson and Stephenson 1972). A significant decline in elevation for 13 intertidal seaweeds at Otter Cliffs also occurred during the 74 year period, with no upward expansion for 20 additional species.

Three major present-day seaweed floristic patterns are evident when comparing percent similarities at Mount Desert Island: (1) the values for individual sites are variable, presumably because of pronounced habitat differences; (2) the mean value for the 28 present study sites is quite low ($\bar{x}$ = 36.8 ± 7.6%); (3) the latter value is much lower than similarity values for multiple northwest Atlantic sites (ca. 51.0–92.0%, $\bar{x}$ = 72.3% ± 6.0%) from Campobello Island, New Brunswick, to Penikese Island, Buzzards Bay, Massachusetts (Mathieson et al. 1996). Thus, there are strong contrasts between intra- and interisland percent similarity patterns, which are important in assessing possible anthropogenic impacts (Anonymous 1992, 1995; Greene et al. 1992) as well as evaluating theoretical considerations regarding island biogeography (Mathieson and Penniman 1986). Further, the frequency distribution patterns shown in Figure 6 show that many taxa are

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(3) inner semi-exposed rocks at Otter Cliffs; (4) Otter Cove; (5) Thompson Island, sheltered bay; (6) exposed rocks of Bald Head (Femino and Mathieson 1980); and (7) semi-exposed Jaffrey Point (Mathieson et al. 1981). Note that five of the species were not found at all seven sites including: *A. nodosum* and *F. vesiculosus* (site 2), *M. stellatus*, *C. crispus*, and *C. circumscriptum* (site 5), and *P. palmata* and *D. ramentacea* (site 4 and 5).

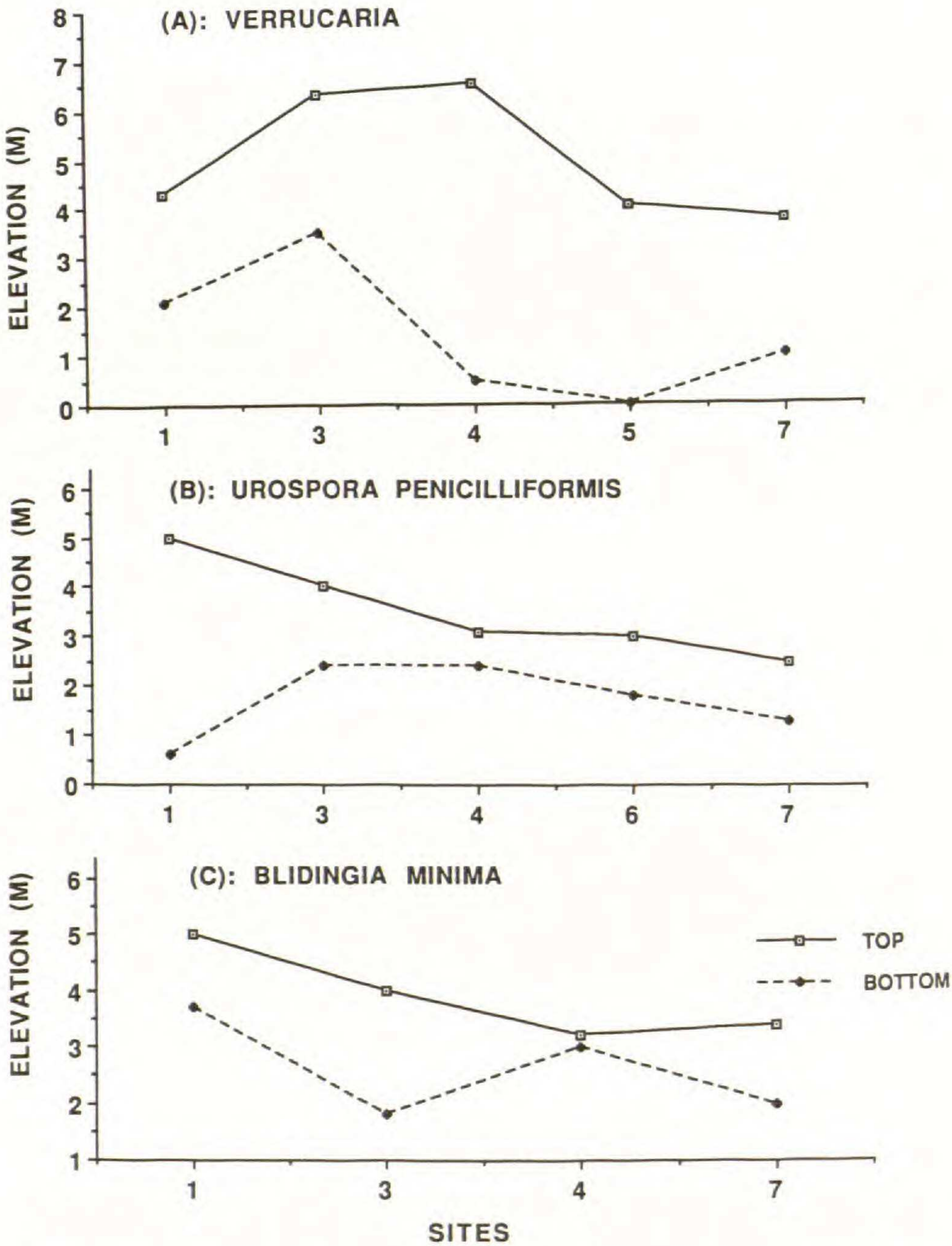

Figure 11. Upper and lower vertical distributions of non-tide pool populations of *Verrucaria* spp. (A), *Urospora penicilliformis* (B), and *Blidingia minima* (C), with site delineations as in Figure 10. The species were not collected at site 2, *Verrucaria* spp. were missing from site 6, *U. penicilliformis* from site 5, and *B. minima* from sites 5 and 6.

Table 3. Difference in upper distributional limits of intertidal seaweeds at Otter Cliffs, Maine, determined from 1923–1927 (Johnson and Skutch 1928a) and 1996. Data for floristic affinities and southern distributional limits are based upon Schneider and Searles (1991), South and Tittley (1986), and Taylor (1957). Key to symbols: Affinities: C = cosmopolitan; N = northern; Southern limits: CT = Connecticut; MA = Massachusetts; NC = North Carolina; NJ = New Jersey; VA = Virginia; * = species showing drop in lower distributional limit.

Species	1928	1996	Difference	Affinities	Limits
CHLOROPHYCEAE					
*Blidingia minima**	5.0 m	4.0 m	−1.0	C	VA
"*Codiolum pusillum*"	4.5 m	4.0 m	−0.5	N	MA
Spongomorpha arcta	2.5 m	0.5 m	−2.0	C	NJ
Urospora penicilliformis	5.0 m	4.0 m	−1.0	C	VA
PHAEOPHYCEAE					
Elachista fucicola	2.5 m	1.5 m	−1.0	C	CT
Fucus distichus ssp. *edentatus*	2.5 m	2.0 m	−0.5	N	MA
*Fucus vesiculosus**	4.5 m	3.0 m	−1.5	C	NC
Laminaria digitata	0.5 m	0.0 m	−0.5	C	CT
RHODOPHYCEAE					
Mastocarpus stellatus	2.5 m	2.0 m	−0.5	C	CT
Palmaria palmata	2.5 m	1.5 m	−1.0	C	NJ
Polysiphonia lanosa	3.0 m	2.5 m	−0.5	C	NJ
Polysiphonia stricta	2.5 m	1.0 m	−1.5	C	NC
*Porphyra umbilicalis**	3.5 m	3.0 m	−0.5	C	VA

cosmopolitan, occurring in diverse open coastal and estuarine sites in New England (Mathieson and Hehre 1986; Mathieson and Penniman 1991).

Several present-day comparisons of Mount Desert and other northwest Atlantic North American insular floras also can be made. Foremost, Mount Desert's macroalgal flora (145 taxa) exceeds the most floristically diverse, smaller islands (Mathieson and Penniman 1986) of Smuttynose Island, Maine (136 taxa), and Penikese Island, Massachusetts (131 taxa); at the same time, its species diversity is considerably less than Newfoundland (ca. 254 taxa), the largest island within this same geography (South 1983; South and Hooper 1980). A comparison of nine smaller islands within contiguous Penobscot Bay (Figure 1) shows a range of 4–65 taxa/island ($\bar{x}$ = 30.8 ± 23.0) and 97 total taxa (Mathieson et al. 1996). Further, Mount Desert's flora exceeds the insular floras of Penobscot Bay, both individually and collectively. In a broader context, Mount Desert's flora is relatively diverse compared with contiguous coastal embayments: (1) 159 taxa for Passamaquoddy Bay, New Brunswick, Canada (Tittley et al. 1987); (2) 139 taxa for Penobscot Bay as a whole, including insular and nearshore sites (Mathieson et al. 1996); (3) ca. 194 taxa for Casco Bay, Maine (Collins 1911; Farlow 1881; Mathieson and Hehre, unpubl. data). Thus, macroalgal diversity can be related to island size, which in turn is correlated with habitat complexity (positively) and anthropogenic impacts (negatively).

With respect to historical floristic comparisons, Otter Cliffs shows an apparent "enhancement" of species richness, Seal Harbor exhibits a conspicuous reduction and Seawall-Southwest Harbor shows approximate equality. The inconsistent patterns might result from several factors: incomplete characterization of Otter Cliffs (Johnson and Skutch 1928a, b, c), temporal variability of the floras (Harris et al. 1998), or anthropogenic effects (e.g., Seal Harbor). Thus, different factors may be important in determining individual patterns. Two of the most conspicuous factors are habitat diversity and frequency of collections. For example, a comparison of the seaweed flora of the semi-exposed Jaffrey Point, New Hampshire, site showed a pattern of maximum species richness (see Figure 9G), presumably because of its "intermediate" environment (Connell 1979), plus the fact that detailed seasonal and spatial collections were made (Mathieson et al. 1981, 1991).

As shown in Table 3, eleven of the thirteen species with altered historical zonation patterns are cosmopolitan, being widely distributed north and south of Cape Cod, Massachusetts. The other two taxa ("*Codiolum pusillum*" and *Fucus distichus* ssp. *edentatus*) are more common north than south of the Cape (South and Tittley 1986; Taylor 1957). It should be emphasized that seaweed zonation patterns can be influenced by abiotic factors such as wave activity (Figures 9–11), as well as varying climatic conditions. For example, in a study of intertidal invertebrates at Monterey Bay, California, Barry et al. (1995) found that 8 out of 9 "southern" taxa showed an increase in abundance between 1931 and 1994. By contrast, 5 of 8 "northern" species decreased in abundance during the same period. Barry et al. suggest that the basis for these changes could be an increase in air and water temperature. In the Gulf of Maine, Harris et al. (1998) reported that several "southern" subtidal invertebrates expanded their distribution between 1979 and 1994, presumably due to an increase in mean seawater temperatures of approximately 1°C during this same period. Introduced taxa included the southern sea star *Asterias forbesi*, the tunicate *Diplosoma* sp., and the exotic green alga *Codium fragile* ssp. *tomentosoides*. The downward shift in elevation of 13 intertidal seaweeds at Otter Cliffs may be caused, in part, by the general warming trend noted in the Gulf of Maine (Harris et al. 1998). However there was no expansion of more "southern" intertidal taxa as reported by Barry et al. (1995). Another possible factor influencing intertidal distribution is increased atmospheric ozone levels. Indeed, high levels of this pollutant have been monitored at Acadia National Park in the 1980s and extensive damage to terrestrial plants, including spreading dogbane, has occurred due to ozone injury (Eckert et al. 1994, 1997).

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APPENDIX

HISTORICAL AND RECENT COLLECTIONS FROM MOUNT DESERT, MAINE, AND ADJACENT CRANBERRY ISLES, INCLUDING SITES, DATES, AND NAMES OF COLLECTORS.

Site:

1. Thompson Island, Mount Desert Narrows, Bar Harbor (Recent: 11/16/1996)
2. Old House Cove, Mount Desert Narrows, Bar Harbor (Recent: 10/6/1994)
3. Hadley Point, Mount Desert Narrows, Bar Harbor (Recent: 4/16/1995)
4. Hulls Cove, Frenchman Bay, Bar Harbor (Recent: 4/3/1995)
5. Town pier, Bar Harbor (Recent: 4/14/1967, 4/14/1968, 1/14/1983, 4/3/1995)

5a. Bar Harbor (Historical: FSC: 7/1896; HWG & GHG: 10/1949; MZ: 8/18/1966)

6. Schooner Head/Anemone Cave area, Bar Harbor (Recent: 4/16/1995, 2/22/1996, 5/5/1996)
7. Great Head, Bar Harbor (Recent: 4/3/1995)
8. Sand Beach, Bar Harbor (Recent: 4/16/1995, 2/22/1996)
9. Old Soaker, Bar Harbor (Recent: 2/22/1996)
10. Thunder Hole, Bar Harbor (Recent: 4/15/1955, 9/25/1981, 2/22/1996, 5/5/1996)
11. Otter Cliffs, Bar Harbor (Historical: FSC: 7/12/1900, 7/17/1900, 7/20/1900; DSJ: 6/1927, 6/5/1927, 6/23/1927, 7/1927, 7/9/1927; DSJ & AFS: 1928 (Msc.); Schramm: 1941; Recent: 9/25/1981, 8/23/1994, 10/25/1996)
12. Otter Point, Bar Harbor (Recent: 4/13/1967, 4/13/1968, 8/25/1994, 4/16/1995, 5/5/1996)
13. Otter Cove, Bar Harbor (Recent: 4/25/1996, 8/23/1996, 10/25/1996)

13a. Otter Creek, Mount Desert (Historical: FSC: 7/12/1900, 7/17/1900, 7/20/1900)

14. Western Point, near Black Woods Campground, Mount Desert (Recent: 5/15/1970, 5/15/1971, 3/25/1995, 2/22/1996)

14a. Hunter's Beach, near Ingraham Point, Mount Desert (Historical: FSC: 7/11/1900, 7/11/1902)

15. Seal Harbor, near Crowninshield Point, Mount Desert (Historical: LRB: 1890; FSC: 7/24/1889, 7/1890, 7/2/1890, 7/22/1890, 8/8/1890, 8/11/1890, 1894 (Msc.), 7/1897, 6/17/1899, 7/1899, 7/15–7/17/1899, 7/14/1900; IH: 8/17/1889; EWR: 8/1888; Recent: 3/25/1995, 4/15/1995, 5/5/1995, 2/22/1996, 9/29/1996)
16. Bracy Cove, Mount Desert (Historical: FSC: 7/22/1889, 7/20/1890; IH: 8/11/1890; Recent: 3/25/1996, 5/5/1996)
17. Northeast Harbor, Mount Desert (Historical: HdR: 8/1903; Recent: 3/25/1995, 2/22/1996)

17a. Little Cranberry Isle, Cranberry Isles (Historical: FSC: 1894 (Msc.), 7/20/1890, 7/21/1890, 7/15/1899, 7/16/1899; JHR: 8/6/1889)

18. Somes Sound, off of Sargent Drive & opposite Acadia Mountain/Norumbega Mountain Viewpoint, Mount Desert (Recent: 3/25/1995)

19. Somesville, near junction of Routes 102 & 198, Mount Desert (Historical: FSC 7/24/1889; WJO 9/25/1912; Recent: 8/24/1994)
20. Somesville, @ Rt. 102 & a tidal stream, Mount Desert (Recent: 3/25/1995)
21. Clark Point near U.S. Coast Guard Facility, Southwest Harbor (Historical: AJB and ETM: 7/26/1952; FSC: 7/24/1889, 7/1897, 7/17/1897; IH: 8/2/1889, 8/12/1889, 8/15/1889, 8/17/1889, 8/2/1890, 8/3/1890, 8/6–8/1890, 8/10/1890; Recent: 3/25/1995)
21a. Greening Island, Southwest Harbor (Historical: IH: 8/7/1890)
21b. Near Wonderland Trail, Southwest Harbor (Historical: AFH: 8/11/1889)
22. Seawall, across from Seawall Campground, Southwest Harbor (Historical: FSC: 7/1897, 7/18/1897; IH: 1883, 7/17/1887, 8/1889, 8/8/1889, 8/10/1889, 8/12/1889, 8/15/1889, 8/17/1889, 8/8/1890, 8/12/1890, 7/1897, 7/18/1897, 3/19/1903; DSJ: 7/1927, 7/9/1927; WRT: 9/5/1920, 8/26/1970; Recent: 8/23/1994, 8/24/1994, 3/25/1995, 4/16/1995, 2/23/1996)
23. Bass Harbor Head Light, Tremont (Recent: 3/25/1995, 2/23/1996)
24. Bass Harbor, @ culvert on Rt. 102, Tremont (Recent: 8/24/1994)
25. Seal Cove, Blue Hill Bay, Tremont (Recent: 4/16/1995)
26. Pretty Marsh Harbor, @ Indian Point Road, Mount Desert (Recent: 4/18/1995)
27. Bartlett Narrows boat ramp, off of Indian Point Road, Mount Desert (Recent: 4/18/1995)
28. Indian Point @ Blagden Preserve, Western Bay, Bar Harbor (Recent: 4/18/1995)
29. Recorded from Mount Desert Island with no specific location (Historical: FSC: 7/1900)

Historical Collectors: AJB: Albert J. Bernatowitz; LRB: L. R. Boggs; FSC: Frank S. Collins; GHG: Gilbert H. Goff; HWG: Helen W. Goff; AFH: Albert F. Hill; IH: Isaac Holden; DSJ: Duncan S. Johnson; ETM: Edward T. Moul; WJO: Winthrop J. Osterhout; EWR: Elisa W. Rand; JHR: John H. Redfield; HdR: H. de Roasloff; Schramm; AFS: Alexander F. Skutch; WRT: William R. Taylor; MZ: Martin Zimmerman.